The Mesofilter Concept and Biodiversity Conservation in Afro-montane Grasslands

by

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Declaration

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Summary

Conservation planners use many traditional biodiversity conservation tools to help alleviate the global biodiversity crisis. However, ongoing biodiversity loss has stimulated the development of new and improved methods for conserving biodiversity. One such new conservation tool is the mesofilter approach. Mesofilters are biotic or abiotic ecosystem elements which are critical to the well-being of many species, and therefore could help to explain spatial heterogeneity in species across a landscape. It is also complementary to more traditionally used concepts such as coarse- and fine-filter conservation concepts. Applying the mesofilter approach in protected area, conservancy, or land-sparing design and management, could optimise biodiversity conservation in a rapidly developing world. For example, the timber industry has been pro-active in its approach to lessen biodiversity loss, by optimising design and management of the plantation matrix through ecological networks. Here, I explore the use of mesofilters within highly threatened remnant Afro-montane grasslands in KwaZulu-Natal, South Africa, to optimise biodiversity conservation planning for such landscapes. As per anecdotal evidence, I used rockiness in the landscape as a possible driver of species richness and species assemblage variability at the meso-scale, using a multi-taxon and multi-trophic approach. In this montane landscape, I also examined the effect of elevation on spatial heterogeneity of taxa. I further examined the functional responses of taxa to rockiness in the landscape. Rockiness in the landscape significantly influenced the species richness and assemblage structure of three key grassland taxa: flora, butterflies, and grasshoppers. I showed that for plants, this response was due to growth forms such as geophytes and perennial grasses that were more closely associated with rockiness, and therefore the main contributors to observed differences in the dispersion patterns of flora. Grasshoppers were not necessarily responding to higher rock exposure *per se*, but rather towards the environmental conditions created by rockiness within the landscape, such as lower vegetation density. For butterflies, certain behavioural traits, such as resting, territorial behaviour and/or mate-locating behaviour, were more typical in areas of higher rock exposure. This suggested that rocks are a definite habitat resource to certain butterflies. Overall, this finding where an abiotic surrogate is representative of key taxa in an ecosystem is interesting, as cross-taxon surrogacy has been shown to be stronger than surrogates based on environmental data. Furthermore, taxa responded functionally to rockiness in the landscape. This thesis therefore supports the idea that environmental surrogates are indeed useful for biodiversity conservation planning. Furthermore, ecosystems can potentially have

many attributes or features that would be of conservation interest, and delineating a set of mesofilters is a useful way of expressing particular attributes to be used in wildlife conservation evaluation. The concept of the mesofilter as a practical biodiversity conservation tool is therefore validated here. I also argue the importance of habitat heterogeneity for biodiversity conservation planning in this montane grassland landscape. The potential for optimising the design of landscape configurations such as ecological networks, through information obtained from the mesofilter, is emphasised. We can safely add another tool in the biodiversity conservation toolbox of this Afro-montane grassland ecosystem.

Samevatting

Bewaringbeplanners gebruik tans baie tradisionele biodiversiteit-bewarings metodes om die huidige biodiversiteits krisis te help verlig. Tog, die huidige voortdurende verliese in biodiversiteit wêreldwyd, vra na nuwer en verbeterde metodes van biodiversiteit-bewaring. Een so 'n nuwe bewaring metode, is die mesofilter. Mesofilters is biotiese of abiotiese ekosisteem elemente wat kritiek is tot die welstand van spesies, en daarom veral waardevol is om variasie in spesies verspreiding in 'n landskap te help verduidelik. Daarby is die mesofilter konsep ook komplementêr tot meer tradisioneel gebruike bewaringskonsepte, soos fyn-filter en breë-filter konsepte. Deur die mesofilter benadering toe te pas in die ontwerp en bestuur van beskermde areas, bewaareas, of land-spaar initiatiewe, kan ons biodiversiteit-bewaring in 'n vining ontwikkelende wêreld optimaliseer. Byvoorbeeld, die bosbou industrie is pro-aktief in hul benadering om biodiversiteit verliese te verminder, deur optimalisering van die ontwerp en bestuur van ekologiese netwerke in die plantasiematriks. In hierdie tesis, ondersoek ek die gebruik van mesofilters in hoogs bedreigde oorblyfels Afrikaberg grasvelde in KwaZulu-Natal, Suid-Afrika, om die bewaringsbeplanning van dié gebiede te optimaliseer. Vanaf anekdotiese bewyse, het ek spesifiek gebruik gemaak van klipperigheid in die landskap as 'n moontlike drywer van spesies-rykheid en spesies-samestelling variasie by 'n meso-skaal, deur 'n multi-takson en multi-trofiese benadering. In hierdie berglandskap, het ek ook die effek van hoogte bo seevlak op ruimtelike verspreiding van taksa bestudeer. Verder het ek ook gekyk na die funksionele reaksie van taksa tot klipperigheid in die landskap. Klipperigheid in die landskap het 'n beduidende invloed gehad op spesies-rykheid en spesies-samestelling van drie sleutel grasveld taksa: plante, skoenlappers, en springkane. Ek wys dat vir plante, hierdie reaksie as gevolg was van spesifieke plantgroeivorme, soos bolplante en meerjarige grasse, se noue verband met klipperigheid, en daarom, dat hierdie groepe die hoof bydraers is tot gesiene variasie in plantspesies verspreiding in die landskap. Vir springkane, was hierdie reaksie nie noodwendig omdat hulle die klippe self gebruik het nie, maar meer as gevolg van die omgewingskondisies geskep deur verhoogde klipperigheid in die landskap, soos laer plantegroei digtheid. Vir skoenlappers, was hierdie reaksie tot klippe as gevolg van sekere gedragskaraktereienskappe, soos rus op klippe, gebied beskerming en/of paarmaat soektog, wat tipies meer gesien was in klipperige omgewings. Dit dui daarop dat klippe 'n definitiewe habitat hulpbron is vir sekere skoenlappers. Oor die algemeen is hierdie bevinding, waar abiotiese surrogate verteenwoordig is van drie sleutel taksa in 'n ekosisteem, baie interessant, siende dat tussen-takson surrogate soms gesien word as sterker as surrogate

gebaseer op omgewingsdata. Verder, taksa het funksioneel gereageer teenoor die klippe in die landskap. Hierdie tesis ondersteun dus die idee dat omgewingssurrogate wel nuttig is vir biodiversiteit-bewaring beplanning. Ekosisteme mag vele potensiele elemente van bewarings belang bevat, maar om sulke elemente as 'n stel mesofilters te klassifiseer, is 'n nuttige manier om spesifieke elemente te gebruik in natuurbewarings evaluasie initiatiewe. Gevolglik word die konsep van die mesofilter as 'n praktiese biodiversiteit-bewaring gereedskapstuk hier bevestig. Ek beredeneer ook die belangrikheid van habitat heterogeniteit vir biodiversiteit-bewaring van hierdie berggrasveld landskap. Die potensiaal vir optimalisering van ontwerp en bestuur van landskap konfigurasies, soos ekologiese netwerke, word beklemtoon. Ons kan met veiligheid nog 'n gereedskapstuk plaas in die biodiversiteit-bewarings gereedskapkis van hierdie Afrikaberg grasveld ekosisteem.

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- The creator of coffee

"Come forth into the light of things, let nature be your teacher"
William Wordsworth

Publication Timeline and Disclaimer

Please note that Chapters 2-5 of this dissertation were written as stand-alone papers (see below), and therefore there is some repetition in the methods and results.

Chapter 2

Crous, C.J., Samways, M.J. & Pryke, J.S. (2012) Exploring the mesofilter as a novel operational scale in conservation planning. *Journal of Applied Ecology* DOI: 10.1111/1365-2664.12012

Chapter 3

Crous, C.J., Samways, M.J. & Pryke, J.S. Associations between plant growth forms and rockiness explain plant diversity patterns across a grassland landscape. (under review)

Chapter 4

Crous, C.J., Samways, M.J. & Pryke, J.S. Grasshopper assemblage response to the rocky mesofilter. (under review)

Chapter 5

Crous, C.J., Samways, M.J. & Pryke, J.S. Differential behavioural responses to higher rock exposure in a landscape can help explain butterfly dispersion patterns. (in preparation)

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Chapter 1

General Introduction

The Global Biodiversity Crisis

As no species is truly independent from another, intact biodiversity is generally associated with more stable and efficiently functioning ecosystems (Naeem *et al*. 1994; Chapin *et al*. 2000; Tilman *et al*. 2006). For example, a global positive relationship between plant species richness and ecosystem multifunction has been recorded for dryland ecosystems (Maestre *et al*. 2012). Yet, there is rapid and on-going fragmentation of the natural environment owing to increased demographic pressure on natural resources (Vitousek *et al*. 1997; Sala *et al*. 2000). Dispersal dynamics of many species are negatively affected, restricting or limiting their recruitment and distribution, which could ultimately lead to extinction of species and losses of ecosystem function (Tilman 1997; see also Pimm *et al*. 1995). Furthermore, a decrease in biodiversity within plant communities, for example, could 1) decrease CO_2 absorption, thereby restricting the current crucial necessity for carbon sequestration (Naeem *et al*. 1994; Williams *et al*. 2008); promote losses in soil nutrients (Tilman *et al*. 1996); and 3) increase invasion potential of alien species (Fargione & Tilman 2005). Essentially biodiversity degradation limits an ecosystem's buffer against temporal variation in environmental conditions, e.g. drought periods (Yachi & Loreau 1999; Rockström *et al*. 2009). In addition, socio-economic advantages, particularly sustainable food and water provision for human consumption, are also strongly linked to intact biodiversity (Pearce & Moran 1994; Thrupp 2000; Chapin *et al*. 2000; Naidoo *et al*. 2011). In essence, conserving biodiversity has significant value for maintaining critical ecosystem processes, as well as subsequent goods and services (Schläpfer *et al*. 1999).

Unfortunately, current loss of biodiversity worldwide is continuing, with a missing of the Convention on Biological Diversity's (CBD) target to significantly reduce biodiversity loss by 2010 (Walpole *et al*. 2009; Butchart *et al*. 2010; Mooney 2010). The CBD has developed a new set of targets for 2020 (The Aichi 2020 Biodiversity Targets). Although not the complete answer for solving the biodiversity crisis (Perrings *et al*. 2010), these targets are positive in that they indicate the ongoing urgency to reduce pressures on biodiversity through sustainable practices. These targets emphasise the development of new and improved methods for conserving biodiversity. This is especially relevant in the modern conservation context,

where most of the earth's surface continues to be transformed (Ellis *et al*. 2010). The maintenance of biodiversity, in general, is therefore a critical conservation objective to ensure sustainable provision of ecosystem goods and services (Hooper *et al*. 2005; Maestre *et al*. 2012). Therefore, ecologically sound management of remnant patches, whether natural or semi-natural, becomes increasingly important.

Remediating the biodiversity crisis

To maintain biodiversity in a rapidly developing world, one of the first needs is to prioritise biotic inventories so we are able to identify biodiversity hotspots or areas of conservation importance (Reid 1998; Myers *et al*. 2000). Secondly, we need to understand the factors, natural or anthropogenic, affecting species distributions in space and time. Indeed, the drivers of species distributions under variable environmental conditions are a highly relevant and an important conservation research topic at present (Richardson 2012). This originates from the assumption that species movement is not random, where many factors play a role in either enhancing species richness in some areas, while prohibiting it in others (Palmer 1994). Exploring the ecological determinants of observed spatial heterogeneity in species richness across multiple scales would greatly improve conservation planning for both biodiversity maintenance (e.g. protected area design) and the movement of species under a changing climate (Gaston 2000). Therefore, studying species distribution patterns at a small spatial scale, in addition to regional biodiversity hotspots, would support protected area design by incorporating biodiversity patterns (Rodrigues *et al*. 2004).

The biodiversity planning toolbox

There exists a variety of popular and effectively applied biodiversity conservation concepts (reviewed by Schulte *et al*. 2006). Of these, predominantly two focal/operational scale conceptual tools are often used to delineate reserve networks or protected areas (Noss 1987; Schwartz 1999; Schulte *et al*. 2006):

- a *fine-filter* approach, which is more directed at creating reserves around genes, species or populations (although often just used for population management)
- a *coarse-filter* approach, which is more directed at using communities, landscapes or ecosystems
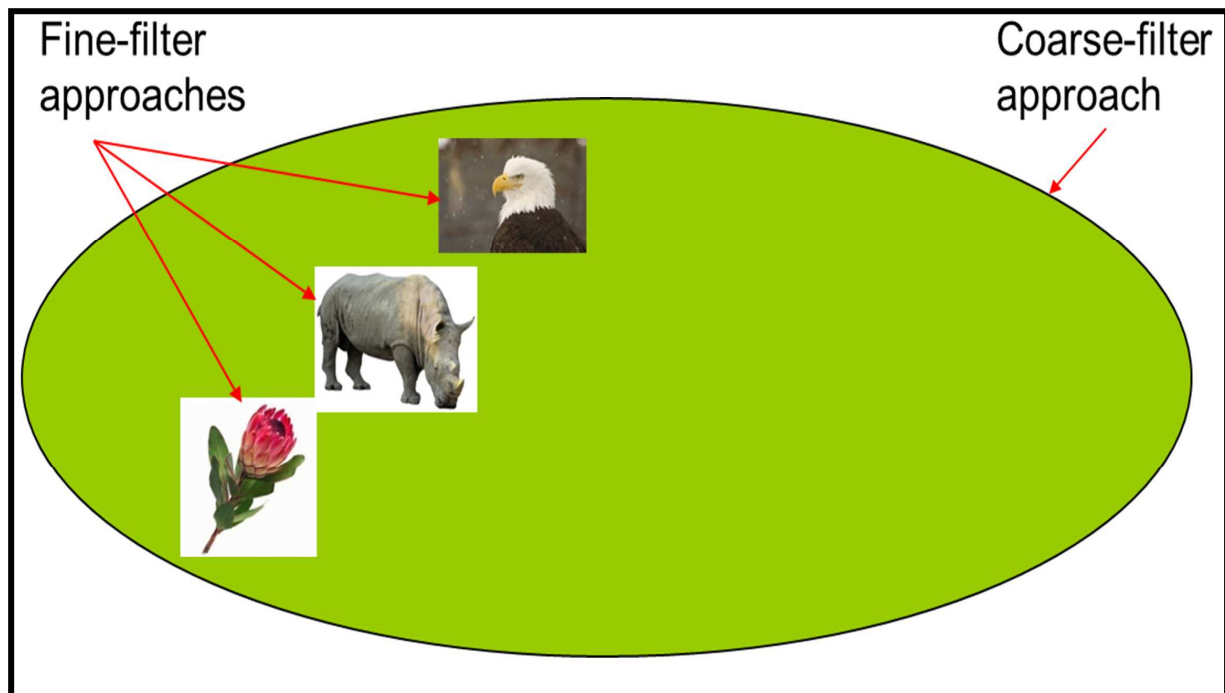
Figure 1.1 A visualization of two traditional focal scale concepts for biodiversity conservation

Fine-filter approaches usually entail the use of surrogates of biodiversity through concepts such as umbrella species, focal species or even guilds, whereas coarse-filter reserve selection is theoretically more directed towards including multiple habitats or a certain area of a specific ecosystems (Fig. 1.1). For example, one could take a conspicuous species, which is highly threatened, and just protect its known habitat. Alternatively, one could take a coarse-filter approach and conserve a highly diverse area which should lead to higher productivity and sustainability within that reserve, as higher diversity areas and sustainability are closely linked (*sensu* Tilman *et al*. 2001; 2006). However, both of these concepts have their shortcomings. For the fine-filter approach, the flagship or umbrella species might not be congruent with other less conspicuous species, therefore excluding such species from a protected area or conservancy. The coarse filter approach may also be too coarse, in that it may exclude highly specialized species which are not as closely associated to the coarse selection of a certain habitat or ecosystem (see Groves *et al*. 2002; also see Chapter 2, p. 17, for more detail on filter conservation). To address these shortcomings, Hunter (2005) developed a new operational scale for biodiversity conservation – the mesofilter. Broadly, the mesofilter can be defined as specified ecosystem elements, or features, which are important to the existence of certain species within an area. The mesofilter *complements* the coarse filter

by helping conservation planners delineate multiple physical features of the landscape which are known to be associated with, and promote, a higher variety of species. It also *complements* fine-filter conservation, by focusing on those ecosystem elements which are easier to survey and map than single species. Given the complementary nature of the newer mesofilter concept to other well studied biodiversity conservation concepts, it needs more exploration, as it shows promise as a valuable addition as an operational scale in the contemporary biodiversity and conservation planning toolbox (Schulte *et al*. 2006; Samways & Böhm 2012).

The Mesofilter (*as per* Hunter 2005)

The word *meso* literally means 'middle' or 'intermediate', and is seen as an intermediate between the fine- and coarse-filter approaches. The key ideas behind a mesofilter are as follows:

- Most ecosystems contain certain biotic or abiotic ecosystem elements which are critical to the well-being of many species
- By conserving these elements in the landscape, you conserve a whole suite of species
- It therefore complements coarse- and fine-filter approaches (as mentioned above), adding to our understanding of ecosystem scale

There are many examples of mesofilters within an ecosystem, and Hunter (2005) lists some examples: logs in a forest, hedgerows in agricultural landscapes, reefs in an estuary, streams, riparian vegetation, pools in terrestrial ecosystems and rocky outcrops. Essentially, we may see the maxim of the mesofilter as abiotic variables acting as surrogates for biota. Many studies have shown certain ecosystem elements or landscape features to be important indicators of diversity, emphasizing that conservation of these elements leads to protection of a diversity of species (Armstrong *et al*. 1994; Armstrong & van Hensbergen 1999; Wessels *et al*. 1999; Hewitt *et al*. 2005; Overton *et al*. 2006; Barton *et al*. 2009; Overton *et al*. 2010). However, if we classify these findings as mesofilter conservation *per se* as posited by Hunter (2005), we could add this practical biodiversity conservation tool to each respective ecosystem's conservation toolbox.

A 2-dimensional landscape. Vegetation type being equal. Which area should have conservation priority?
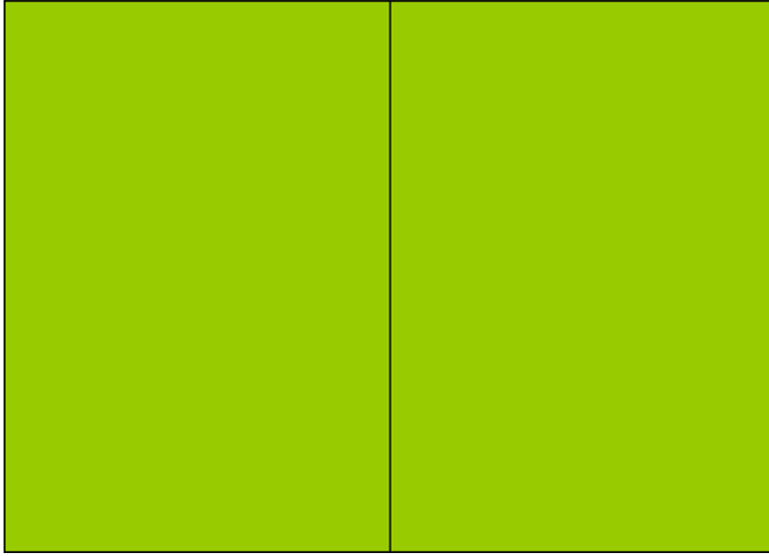
Lets add a third layer to the landscape—mesofilters, such as woody logs and a riverine system, for example
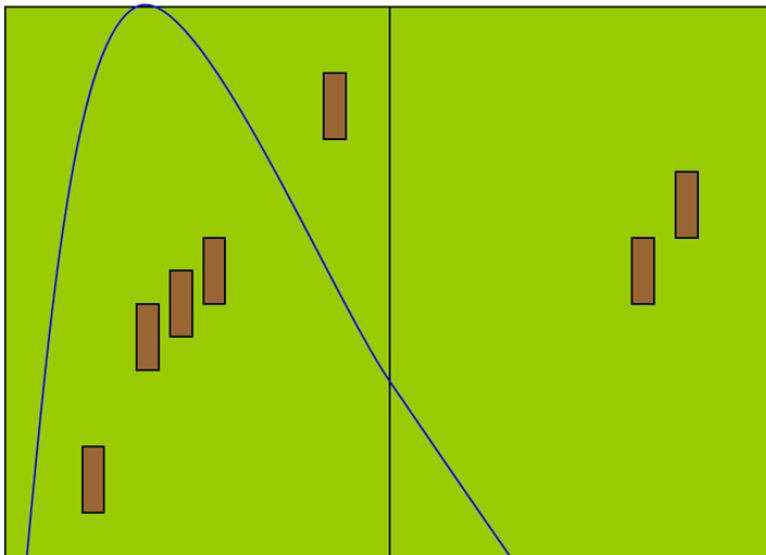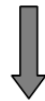
A better informed reserve design or management decision can now be made. The left panel, in this instance, suggests higher biodiversity value.

Figure 1.2 A simplified example of application of the mesofilter concept in delineating reserves or managing an area for biodiversity conservation purposes where development is taking place rapidly

Applying the mesofilter in contemporary conservation

Much of the earth's surface is already transformed through agriculture, urbanization etc. (Ellis *et al*. 2010). In that light, it becomes apparent that, in many instances, we cannot any longer set aside whole ecosystems for conservation. However, the ideal is to create a 'win-win' situation, e.g. in agriculture and conservation, which would lead to sustainable agroecosystems in a fast developing world (Power 2010). The mesofilter approach encourages us to consider optimal biodiversity conservation in such dynamic environments. For example, the mesofilter is complementary towards coarse-filter approaches where we cannot set aside whole ecosystems, and complementary towards fine-filter approaches, where many species will not be targeted for species specific management (Fig. 1.2). Essentially, this mesofilter approach to conservation adds another dimension to the 2-dimensional nature of landscapes (*as per* Samways 1990). Not only is this important for reserve design and management, but also for areas outside of protected areas, such as local conservancies (i.e. matrix management).

The mesofilter concept in Afro-montane grassland remnants within a forestry matrix

Plantation forestry is known to negatively impact biodiversity (Armstrong *et al*. 1998; Richardson 1998; Lindenmayer *et al*. 2003). The production of timber causes both land-use change and, in many instances, biotic introductions, which is why the timber industry has received so much attention from conservation agencies. The grassland biome in South Africa occupy ca. 13.3% of the country's area (Cowling *et al*. 1989), and plantation forestry is seen as a significant driver of the critically endangered status of vegetation types within this biome (Neke & Du Plessis 2004; Mucina & Rutherford 2006). However, plantation forestry in South Africa contributes to a great deal of the production landscape, and is an essential part of South Africa's economy. Fortunately, commercial operations, such as plantation forestry, are required to be environmentally sensitive. In this light, the timber industry has proved to be proactive in its approach to lessen its impact on the environment through research pertaining to protecting the remnant natural or semi-natural areas in the forestry matrix (see also Hartley 2002; Lindenmayer *et al*. 2003). More specifically, most of the industry strives to optimise the design and management of the plantation matrix through ecological networks (Samways *et al*. 2010). As simplified in Fig. 1.2, delineating certain mesofilters within a landscape can

thus significantly contribute in our design and management of landscape configurations such as ecological networks (Schulte *et al*. 2006).

The Aims and Outlines of this Dissertation

Problem statement

In this brief introduction, we can see that perceptions on agricultural production are changing considerably, with an emphasis on a sustainable supply chain, from producer through to consumer. Indeed, these changes are being required by Europe and other markets under pressure from consumers requiring South African agricultural products to be produced in a way that is healthy and environmentally sensitive. So for these industries to remain competitive, they have to adequately conserve biodiversity. These companies need the tools to help make rapid biodiversity management decisions.

Rationale

Stellenbosch University, and the Designing Future Landscapes Initiative, has developed a set of principles to improve the sustainability of the supply chain, with particular emphasis on biodiversity conservation and ecosystem processes pertaining to production of agricultural and forestry products that are being demanded by certification processes (Samways 2007). Here, I explore an additional operational scale, the mesofilter, which could improve the direct linkages between research and the corporate production sector. This thesis aims to investigate the practical application of the mesofilter concept in potential design and management of the landscape for optimal production without compromising biodiversity.

Proposed mesofilter

A conservation evaluation of afforestable montane grasslands in South Africa by Armstrong *et al*. (1994) indicated that a level of rock exposure within a landscape probably influences the species richness of both flora and butterflies. However, their study was merely descriptive with no statistical power of the assumptions made. Upon further investigation in another

montane grassland area, it was apparent that the landscape is a matrix of rocky and less rocky areas (Fig. 1.3). From personal observation, I also saw some apparent differences in plant species richness of the rocky areas. Given these preliminary findings, and seeing as these rocks are key ecosystem elements which are relatively durable through geological time, the question arose: could these rocks be a major influence in structuring key grassland taxa, and thus be classified as a mesofilter for this Afro-montane grassland?
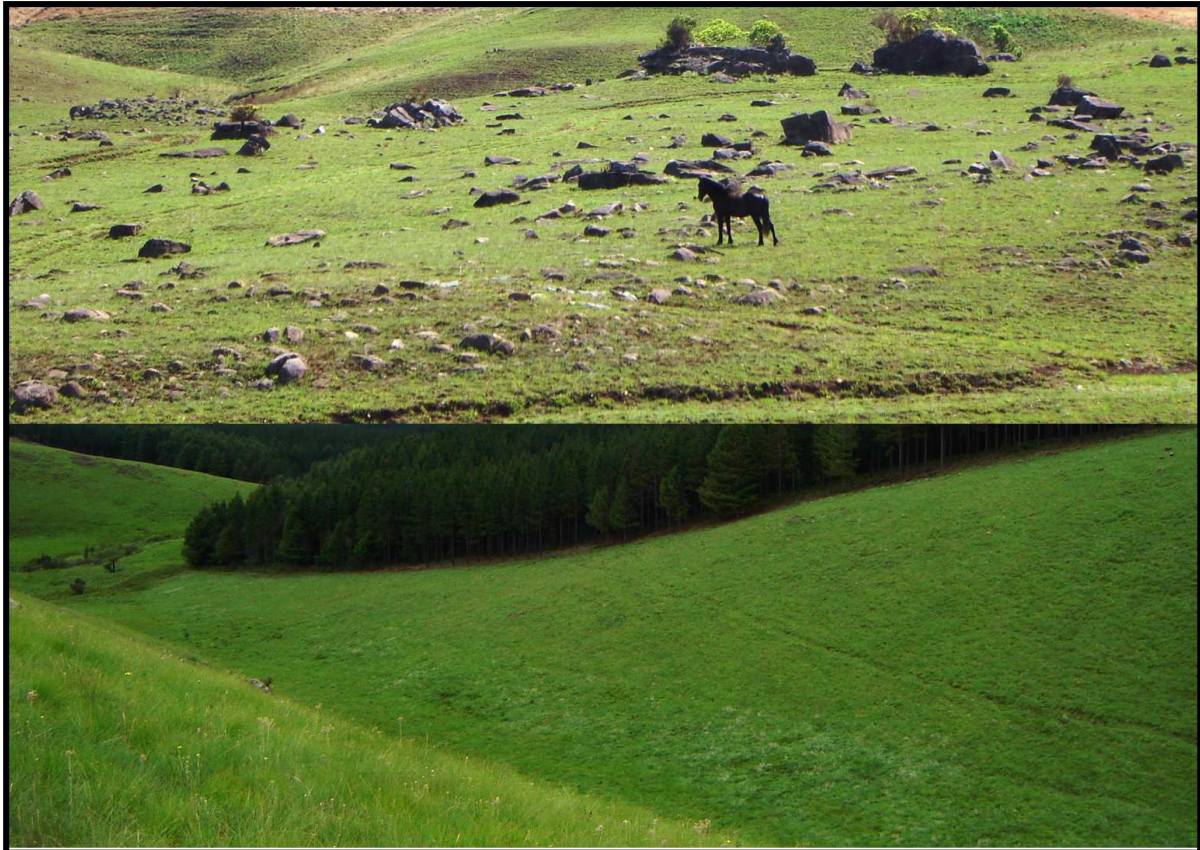
Figure 1.3 An example of the greatly rocky and lesser rocky nature of sites in my study area

Thesis layout

GENERAL THEME:

Exploring mesofilters (abiotic ecosystem elements) as indicators of species richness and species assemblage variability at a landscape scale, using a multi-taxon and multi-trophic approach, to aid in conservation planning. Specifically, I aim to establish **if** specific ecosystem elements contribute to species community structure (existence of a mesofilter), and

then **why** these elements are potentially good indicators of species richness and communities (function and behaviour).

The '**if**' part of the study will be explored in *Chapter 2*, where I specifically ask:

1. If a mesofilter, in this instance percentage rock exposure across a landscape (juxtaposed to elevation as a proxy for microclimatic elements), can predict patterns of varying species richness across a landscape scale using a multi-taxon approach.
2. If, in addition to just analysing species richness, this ecosystem element also influences species assemblage composition across this space.
3. If rockiness in a landscape could add another dimension or layer to the design and management of biodiversity conservation plans within the landscape
4. If there is relevance in implementing this approach considering other currently implemented conservation strategies such as coarse- and fine-filter approaches

Building on from Chapter 2, I ask the '**why**' part of the study in *Chapters 3*, *4*, and *5*

In *Chapter 3*:

1. Why is higher plant species richness associated with higher rockiness in this landscape?
2. Is this a plant functional response to habitat heterogeneity caused by various levels of rockiness?

In *Chapter 4*:

1. Why do grasshopper assemblages respond to a rocky mesofilter?
2. Do they respond to the rockiness *per se*?
3. Is this response limited to certain families or subfamilies?

In *Chapter 5*:

1. Why do higher levels of rock exposure in a landscape structure different butterfly assemblages?
2. Is this pattern consistent with differential behavioural responses to rocks in a landscape?

The conclusions of the study will be discussed in *Chapter 6*, where I specifically discuss:

1. Whether the mesofilter is a viable method for determining micro-biodiversity hotspots within an agricultural landscape, across multiple taxa.

2. How we can apply the mesofilters tested in reserve design and management, as well as for conservancies outside of formally protected areas.

References

Armstrong, A.J., Benn, G., Bowland, A.E., Goodman, P.S., Johnson, D.N., Maddock, A.H. & Scott-Shaw, C.R. (1998) Plantation forestry in South Africa and its impact on biodiversity, *The Southern African Forestry Journal*, **182**, 59-65

Armstrong, A.J. & van Hensbergen, H.J. (1999) Identification of priority regions for animal conservation in afforestable montane grasslands of the northern Eastern Cape Province, South Africa. *Biological Conservation*, **87**, 93-103

Armstrong, A.J., van Hensbergen, H.J. & Geertsema, H. (1994) Evaluation of afforestable montane grasslands for wildlife conservation in the north-eastern Cape, South Africa. Part 1. Methods. *South African Forestry Journal*, **171**, 7-20

Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Cunningham, S.A. (2009) Conserving ground-dwelling beetles in an endangered woodland community: multi-scale habitat effects on assemblage diversity. *Biological Conservation*, **142**, 1701-1709

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Hernández Morcillo, M., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J-C. & Watson, R. (2010) Global Biodiversity: Indicators of Recent Declines. *Science*, **328**, 1164

Chapin, F.S., III, Zaveleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Lavorel, S.,

Reynolds, H.L., Hooper, D.U., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, **405**, 234-242

Cowling, R.M., Gibbs-Russel, G.E., Hoffman, M.T. & Hilton-Taylor, C. (1989). Patterns of plant species richness in Southern Africa. In Huntley BJ (ed.) *Biotic Diversity in Southern Africa: concepts and conservation*. Oxford University Press, Cape Town.

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589-606

Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604-611

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227

Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., Baumgartner, J.V., Higgins, J.V., Beck, M.W. & Anderson, M.G. (2002) Planning for biodiversity conservation: putting conservation science into practice. *BioScience*, **52**, 499-512

Hartley, M.J. (2002) Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management*, **155**, 81-95

Hewitt, J.E., Thrush, S.E., Halliday, J. & Duffy, C. (2005) The importance of small-scale habitat structure for maintaining beta-diversity. *Ecology*, **86**, 1619-1626

Hooper, D.U., Chapin, III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3-35

Hunter, Jr., M.L. (2005) A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology*, **19**, 1025-1029

Lindenmayer, D.B., Hobbs, R.J. & Salt, D. (2003) Plantation forests and biodiversity conservation. *Australian Forestry*, **66**, 62-66

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-Gonzáles, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-

Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D. & Zaady, E. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science*, **335**, 214-218

Mooney, H.A. (2010) The ecosystem-service chain and the biodiversity chain. *Philosophical Transactions of the Royal Society B*, **365**, 31-39

Mucina, L. & Rutherford, M.C. (eds) (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria

Myers, N., Mittermeier, R.A., Mittermeier, C.G., de Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734-737

Naidoo, R., Weaver, L.C., Stuart-Hill, G. & Tagg, J. (2011) Effect of biodiversity on economic benefits from communal lands in Namibia. *Journal of Applied Ecology*, **48**, 310-316

Neke, K.S. & Du Plessis, M.A. (2004) The threat of transformation: quantifying the vulnerability of grasslands in South Africa. *Conservation Biology*, **18**, 466-477

Noss, R. (1987) From plant communities to landscape in conservation inventories: a look at the Nature Conservancy (USA). *Biological Conservation*, **41**, 11-37

Overton, C.T., Casazza, M.L. & Coates, P.S. (2010) Scale association of Band tailed pigeon counts at mineral sites. *Northwestern Naturalist*, **91**, 299-308

Overton, C.T., Schmitz, R.A. & Casazza, M.L. (2006) Linking landscape characteristics to mineral site use by Band-Tailed Pigeons in Western Oregon: coarse-filter conservation with fine-filter tuning. *Natural Areas Journal*, **26**, 38-46

Palmer, M.W. (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica & Phytotaxonomica*, **29**, 511-530

Pearce, D.W. & Moran, D. (1994) *The Economic Value of Biodiversity*. Earthscan Publications, London

Perrings, C., Naeem, S., Ahrestani, F., Bunker, D.E., Burkill, P., Caniani, G., Elmqvist, T., Ferrati, R., Furhman, J., Jaksic, F., Kawabata, Z., Kinzig, A., Mace, G.M., Milano, F., Mooney, H., Prieur-Richard, A.H., Tschirhart, J. & Weisser, W. (2010) Ecosystem services for 2020. *Science*, **330**, 323-324

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995). The Future of Biodiversity. *Science*, **269**, 347-350

Power, A.G. (2010) Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B*, **365**, 2959-2971

Reid, W.V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13**, 275-280

Richardson, D.M. (1998) Forestry trees as invasive aliens. *Conservation Biology*, **12**, 18-26

Richardson, D.M. (2012) Conservation biogeography: what's hot and what's not? *Diversity and Distributions*, **18**, 319-322

Rockström, J., Steffen, W., Noone, K., Persson, Å, Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen P. & Foley, J.A. (2009) A safe operating space for humanity. *Science*, **461**, 472-475

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. & Yan, X. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, **428**, 640-643

Sala, O. E., Chapin, III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774

Samways, M.J. (1990) Land forms and winter habitat refugia in the conservation of montane grasshoppers in southern Africa. *Conservation Biology*, **4**, 375-382

Samways, M.J. (2007) Insect conservation: a synthetic management approach. *Annual Review of Entomology*, **52**, 465-487

Samways, M.J., Bazelet, C.S. & Pryke, J.S. (2010) Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation*, **19**, 2949-2962

Samways, M.J. & Böhm, M. (2012) Hidden in plain view: effective invertebrate conservation

for our future world. In: Collen, B., Kemp, R. & Baillie, J.E.M. (eds), *Spineless: status and trends of the world's invertebrates*, Zoological Society of London, UK

Schläpfer, F., Schmid, B. & Seidl, I. (1999) Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos*, **84**, 346-352

Schulte, L.A., Mitchell, R.J., Hunter, Jr., M.L., Franklin, J.F., McIntyre, R.K. & Palik, B.J. (2006) Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S. *Forest Ecology and Management*, **232**, 1-11

Schwartz, M.W. (1999) Choosing the appropriate scale of reserves for conservation. *Annual Review of Ecology and Systematics*, **30**, 83-108

Thrupp, L.A. (2000) Linking agricultural biodiversity and food security: the valuable role of agrobiodiversity for sustainable agriculture. *International Affairs*, **76**, 265-281

Tilman, D. (1997) Community invisibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81-92

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843-845

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718-720

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of earth's ecosystems. *Science*, **277**, 494-499

Walpole, M., Almond, R.E.A., Besançon, C., Butchart, S.H.M., Campbell-Lendrum, D., Carr, G.M., Collen, B., Collette, L., Davidson, N.C., Dulloo, E., Fazel, A.M., Galloway, J.N., Gill, M., Goverse, T., Hockings, M., Leaman, D.J., Morgan, D.H.W., Revenga, C., Rickwood, C.J., Schutyser, F., Simons, S., Stattersfield, A.J., Tyrrell, T.D., Vié, J-C., & Zimsky, M. (2009) Tracking progress toward the 2010 biodiversity target and beyond. *Science*, **325**, 1503-1504

Wessels, K.J., Freitag, A.S. & van Jaarsveld, A.S. (1999) The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biological Conservation*, **89**, 21-38

Williams, M., Ryan, C.M., Rees, R.M., Sambane, E., Fernando, J. & Grace, J. (2008) Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique. *Forest Ecology and Management*, **254**, 145-155

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences: USA*, **96**, 1463-1468

Chapter 2

Exploring the mesofilter as a novel operational scale in conservation planning

Abstract

Increased emphasis is being placed on developing effective biodiversity conservation tools for practical conservation planning. The mesofilter is such a biodiversity planning tool, but has yet to be fully explored to appreciate its effectiveness. The key premise of the mesofilter is that ecosystems contain certain physical elements which are specifically associated with a diversity of species. Identifying such mesofilters could therefore complement existing conservation planning tools such as coarse- and fine-filters. To explore the value of the mesofilter as an operational scale in conservation planning, I studied 18 remnant patches of endangered montane grassland in KwaZulu-Natal, South Africa, using the physical landscape feature of patch rockiness as an abiotic surrogate for biodiversity. The objective was to determine whether the mesofilter of rockiness can predict variation in species richness and composition for three dominant grassland taxa (plants, butterflies and grasshoppers) at the landscape scale. Variable levels of rockiness had significant interactions with all three focal taxa. Higher species richness of all taxa was closely associated with higher levels of rockiness in a patch. The rocky mesofilter only predicted significant differences in species composition for butterflies. Elevation was also important, possibly another mesofilter for plants and grasshoppers in this landscape. The results indicate that the use of an abiotic surrogate such as rockiness can predict biodiversity value across multiple taxa. The mesofilter is therefore a valuable surrogacy and congruency tool for practical biodiversity conservation across this landscape, and would likely have similar value if explored elsewhere. It also has value in the design and management of protected areas.

Introduction

One of the main goals of systematic conservation planning is to encapsulate the complexity of biodiversity across different spatial scales and geographical regions when delineating a protected area (Margules & Pressey 2000; Pressey *et al*. 2007). To address this complexity, many biodiversity conservation tools have been developed. These focus on designating a protected area using different species and habitat heterogeneity concepts (Schulte *et al*. 2006). Of these, fine- and coarse-filter operational scales are often used to delineate networks of protected areas (Noss 1987; Schwartz 1999). Protected areas are either designated for a specific species, usually a flagship one, or around a certain set geographical area, e.g. 1000 km^2 of a certain ecosystem (Noss 1987). However, both these fine- and coarse-filter operational scales have their shortcomings.

Fine-filter approaches usually entail the use of surrogates of biodiversity through concepts such as umbrella species, focal species or even guilds (Marcot & Flather 2007). However, congruency issues arise when these surrogates do not adequately represent targeted taxa or overall biodiversity (van Jaarsveld *et al*. 1998; Lindenmayer *et al*. 2002). This means that using focal species as a proxy to protect other taxa could be problematic, since species-specific requirements towards habitat conditions, and their response towards threats, are highly variable in space and time (Lindenmayer *et al*. 2002). Also, areas which are poorly surveyed might lead to false-absence of a species, and consequently be mistakenly excluded from protected areas (Ferrier 2002). Therefore, in many circumstances, fine-filter conservation is not the appropriate approach, since what is needed is to select surrogates (and subsequently protected areas) in such a way that it will also ensure that spatial autecological requirements of most species are met (Margules & Pressey 2000).

In contrast, coarse-filter reserve selection is theoretically more directed towards including multiple ecosystem types or cover types. However, the problem with coarse-filter approaches is that in most cases a lack of knowledge may lead to protected areas not being truly representative of natural ecosystems (Margules *et al*. 1988) and in doing so fail systematic conservation planning. Therefore, for many protected areas to persist, they often need to be expanded into the surrounding matrix to encompass these spatial autecological deficiencies. This can be problematic due to ongoing human infrastructure development (Maiorano *et al*. 2008).

To address this disparity in conservation planning, Hunter (2005) developed a new operational scale for biodiversity conservation – the mesofilter. Broadly, the mesofilter can be defined as specified ecosystem elements, or features, which are important for the maintenance of certain species within an area. The mesofilter complements the coarse-filter by helping conservation planners to delineate those physical features of the landscape which are known to be associated with, and promote, a higher diversity of species (Hunter *et al*. 1988). Furthermore, the conservation significance of using this complementary approach to conservation planning is highlighted, since many mesofilters could also endure over long periods, despite climate change (Hunter *et al*. 1988). Therefore, this mesofilter approach at least partly overcomes the flaw in fine-filter conservation, by focusing on those ecosystem elements which are easier to survey and map than single species. Conversely, instead of using biotic components as surrogates for other biota, the emphasis here is on the use of abiotic elements as surrogates for biota (Carroll 1998). The mesofilter ensures that protected area selection, as well as selecting conservancies outside protected areas, incorporates multiple environmental elements within the geographical area to ensure more comprehensive conservation of biodiversity, compared to an area adjacent or nearby which lacks these elements.

However, the mesofilter concept has not to date received much attention as an operational scale in conservation planning. Many studies have shown certain habitat elements or landscape features to be important indicators of diversity, emphasizing that conservation of these elements leads to protection of a diversity of species (Armstrong *et al*. 1994; Armstrong & van Hensbergen 1999; Wessels *et al*. 1999; Hewitt *et al*. 2005; Overton *et al*. 2006; Barton *et al*. 2009; Overton *et al*. 2010). Barton *et al*. (2009) for example showed that woody logs in a reserve area had specific associations with many beetle species. These logs increased the biodiversity of the area, so delineating beetle biodiversity hotspots. This is important for protected area design and management, as incorporating these logs as part of the conservation planning will increase biodiversity at the landscape level. Therefore, the mesofilter provides a practical approach to inventorying landscape features of increased biodiversity value, to which subsequent management could be directed (Lindenmayer *et al*. 2008). Similarly, should a new protected area network be designed, identifying habitat elements that provide a characteristic assemblage of species would prove a vital addition to the design of the conservation network. The efficacy of using a similar complementary approach when designating biodiversity hotspots within a protected area has been shown (Noss *et al*. 2002).

Recognizing mesofilter conservation *per se*, as posited by Hunter (2005), therefore needs to be explored, particularly as it shows promise as a valuable new operational scale in the biodiversity and conservation planning toolbox (Schulte *et al*. 2006; Samways *et al*. 2010).

In South African montane grasslands, Armstrong *et al*. (1994) provided some evidence that rockier landscapes had higher plant and butterfly species richness. Here I assess the value of mesofilters for conservation planning by looking at this rocky mesofilter. To achieve this, I explore whether percentage rockiness in this case (juxtaposed to elevation as a proxy for microclimatic variation) can predict patterns of varying plant, butterfly and grasshopper species richness at the landscape scale, and in addition to species richness, determine the influence of these habitat characteristics on the similarity of species assemblages across this landscape. These three taxa were chosen as they are among the most dominant in the area, can be sampled in fairly large numbers, and finally, represent three trophic types (primary producer, herbivore and nectarivore).

Methods

Study area

The study was conducted within the 16 000 ha Merensky Forestry estate at Weza, near Kokstad, KwaZulu-Natal, South Africa (S 30°34.855, E 029°44.726; Fig. 2.1). Around 4 200 ha are semi-natural open spaces, the remainder being commercial forestry. The open spaces lie mostly within the endangered Midlands Mistbelt Grassland vegetation type (Mucina & Rutherford 2006). The endangered status of this vegetation type is mainly driven by large forestry plantations and activities in the area. The dominant grass in the area is *Themeda triandra* Forssk. All selected sites are classified as semi-natural, as all were annually burned by forestry management over six decades. Moreover, grazing is limited within these remnants, and fire is consequently seen as the main 'herbivore' (Bond & Keeley 2005). To avoid pseudoreplication, sites of higher rockiness were interspersed with those of lower rockiness across the study area, with the minimum distance between similar sites being 400 m. In addition, all sampling was done >30 m away from the pine forest edge, to reduce sampling bias due to edge effects (Samways & Moore 1991; Bieringer & Zulka 2003; Pryke & Samways 2012).

Flora sampling

Eighteen flora sampling sites were selected. Sampling was done between January and February 2011 (Armstrong *et al*. 1994), through a fixed grid sampling design, where sampling is taken at fixed intervals along a determined gradient (Whalley & Hardy 2000). This design is relatively easy to perform in the field, and has been shown to obtain data rapidly on species distribution and abundance within a study area (Tucker *et al*. 2005). Within this design, I used point intercept line transects, as this method has been shown as relevant and insightful for biodiversity studies in these grasslands (Everson & Clarke 1987; Armstrong *et al*. 1994).
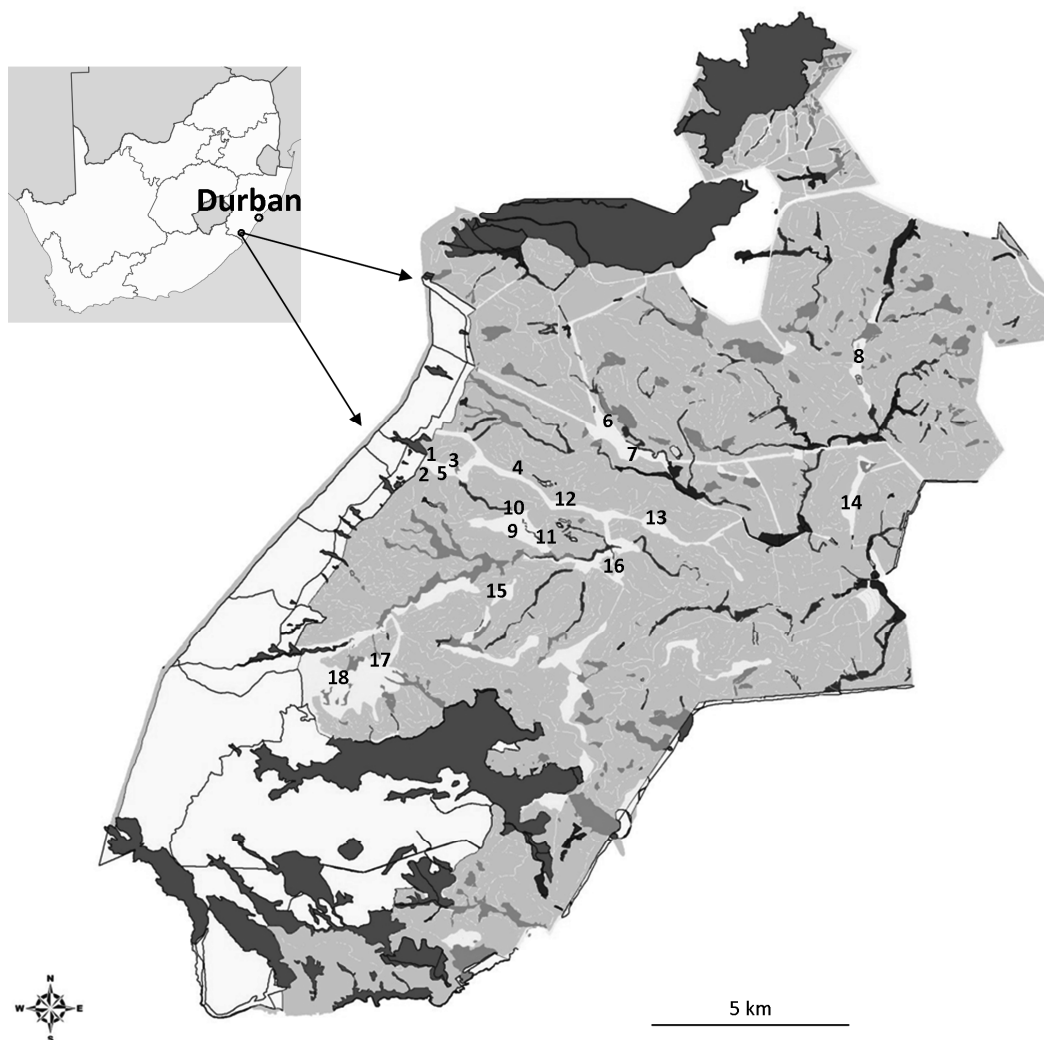
Figure 2.1 Location of the Merensky Forestry estate at Weza, KwaZulu-Natal province, South Africa. Indicated numerically are the sampling sites, all within the open semi-natural grassland areas

Field methods were similar to Hayes and Holl (2003), where a measuring tape, 50 m long, was used to record all plant species that intercept a 1.8 mm-diameter pin every 1 m (51 points per transect). For grasslands, a dense vegetation type, transects of 50 m are seen as adequate (Rich *et al*. 2005). A total of four 50 m transects were placed within each of the eighteen sites, each transect being 15 m away from another, effectively having 204 points per site. Percentage rockiness was obtained by adding the number of times a rock (any rocky surface greater than 10 cm in diameter) touched the pin (exposed rock rather than soil covered rock), divided by the total number of pin hits per transect. Also, a metal stake (36 cm in length) was inserted in the ground every 5 m on each transect, giving 40 depth measurements per site, which serves as a composite indicator of surface rockiness (Stohlgren & Bachand 1997). I then correlated the soil depth with percentage rockiness to ensure correct classification of the site as rocky, and not just a rocky outcrop within a non-rocky matrix.

In addition, a one meter belt, perpendicular to the line transect, was time-searched for 15 minutes after each transect measurement, as a means for recording a more comprehensive species list that could include short lived annual plants (Hayes & Holl 2003).

Butterfly sampling

Butterfly sampling was at the same 18 sites as the flora sampling. Butterflies were sampled twice, in January and April 2011, to encompass seasonal differences. They were sampled within a 50 m radius from the middle point of each site, by two observers facing opposite directions. Each observation unit was 30 min, and replicated over three different days, at three different times of the day, making 90 min search time per person per site (3 hr total per site). Sampling was between 09h00 and 15h00, on warm or hot days (average temperature of 30.2°C for January counts, and 24.7°C for April counts) with <5% cloud cover. To obtain butterfly species richness per site, observations from all replicates were pooled.

Grasshopper sampling

Grasshopper sampling was at the same 18 sites as the flora and butterfly sampling. Sampling was twice, January and April 2011, to cover seasonal differences. Grasshoppers were sampled by sweep netting, which for short dense vegetation types such as grasslands, is adequate (Gardiner *et al*. 2005). Two 100 m transects were laid out. Parallel to each side of each

transect, one hundred 180˚ sweeps were made with a mesh net (diameter 40 cm). This rendered 200 sweeps per transect, and ultimately 800 sweeps per site across the study period.

Statistical analysis

To ensure adequate taxon representation, sampling was conducted until the species accumulation curve nearly flattened (Gotelli & Colwell 2001) (Appendix B). Data were then divided into two sets: continuous data for regression analysis and generalised linear modelling, and categorical data for analysis of variance (ANOVA) and permutational multivariate analysis of variance (PERMANOVA) statistics. Pertaining to categorical data, both the rockiness and elevation values were tested for normality and their variances tested for homogeneity using a Shapiro-Wilk test (Statistica Release 10, StatSoft, Inc.). In both instances the points were normally distributed around the means. As such, there were no distinct groups, and percentage rockiness was presented as a binary classification based on areas having more or less than 10% rockiness, as this was close to the average percentage rockiness measured across the 18 study sites (data not shown). Similarly, elevation was presented as a binary classification established at higher or lower than 1280 m a.s.l., as this was the average measured elevation across the 18 study sites (data not shown). The data were also categorised in this instance to have a practical example of possible implementation in the field.

To examine the overall relationships between richness of all recorded species per site and the measured environmental variables, scatterplots reporting r-values were constructed (Statistica Release 10, StatSoft, Inc.). Similarly, to observe the relationship between each taxon and the measured environmental variables, scatterplots reporting r-values were constructed. To further explore the contribution of the environmental variables on species richness and abundance, I made use of generalized linear models (GLZ) (McCulloch *et al*. 2008) in Statistica Release 10 (StatSoft, Inc.). For flora and grasshopper species richness, each GLZ had a normal distribution and an identity-link function. For butterfly species richness a Poisson distribution with a log-link function was used. For abundance data, all tests were done with a Poisson distribution and a log-link function.

To examine the possible combination of factors driving differences in species richness in space, the dataset was then divided into four groups with regards to habitat rockiness and elevation. These groups were: high (elevations >1280 m a.s.l.) with >10 (areas with more than

10% habitat rockiness), high (elevations >1280 m a.s.l.) with <10 (areas with less than 10% habitat rockiness), low (areas <1280 m a.s.l.) with >10 (areas with more than 10% habitat rockiness) and low (areas <1280 m a.s.l.) with <10 (areas with less than 10% habitat rockiness). Species richness for all measured taxa across these groups was compared statistically using a factorial ANOVA followed by a Fisher LSD post-hoc test (Statistica Release 10, StatSoft) to identify any between group differences. Data were transformed where necessary to adhere to statistical models.

Finally, to explore whether differences in species composition across study sites (if any) could be a function of habitat rockiness or elevation, I used CANOCO 4.5 (ter Braak & Šmilauer 2002) and PERMANOVA (Anderson 2001) in PRIMER 6 (PRIMER-E 2008). In CANOCO I made use of canonical correspondence analysis (CCA) to explore the overall effect of percentage rockiness and elevation on taxa assemblage composition. I also overlaid species richness as a descriptive supplementary variable on each CCA. Forward selection during the CCA analysis was used to rank the most important environmental variables that structure species distribution within each taxon. I used PERMANOVA to study whether there were differences in species assemblage composition across our experimental rockiness and elevation categories. For this statistical method I used an overall test, comparing species composition across each factor (rockiness and elevation), and pairwise tests (comparing species composition within different levels of both factors combined, with categories parallel to the ones used for the species richness ANOVA test). PERMANOVA results are reported as *P*-values (e.g. McNatty *et al.* 2009), where a significant *P*-value indicates a significant difference between two levels (groups) of a studied factor. Analyses were performed using Bray-Curtis similarity measures where data for each taxon was fourth-root transformed to reduce the weight of the common species (Anderson 2001).

Results

Species richness and abundance across environmental variables

A total of 317 plant species (6 574 individuals), 47 butterfly species (551 individuals) and 48 grasshopper species (864 adult individuals) was sampled. Overall, percentage rockiness showed a strong positive correlation with total species richness per site (three taxa combined)

(r = 0.84, *P* < 0.001) whereas elevation showed no significant correlation (r = -0.38, *P* = 0.12) (Fig. 2.2). Percentage rockiness also had no relationship with elevation (r = -0.08, *P* = 0.76) (Fig. 2.2). More specifically, percentage rockiness explained a significant part of the variance observed in both flora (r = 0.806, *P* < 0.05) and butterfly (r = 0.791, *P* < 0.05) species richness across the study sites (Fig. 2.3). Elevation had a statistically significant relationship only with grasshoppers (r = -0.514, *P* < 0.05) (Fig. 2.3).
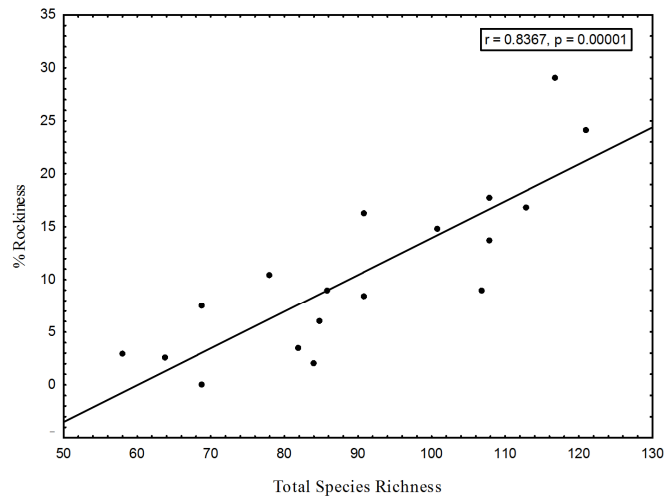
Figure 2.2 The relationships between % rockiness, elevation and the total number of plant, butterfly and grasshopper species recorded at each site. n = 18
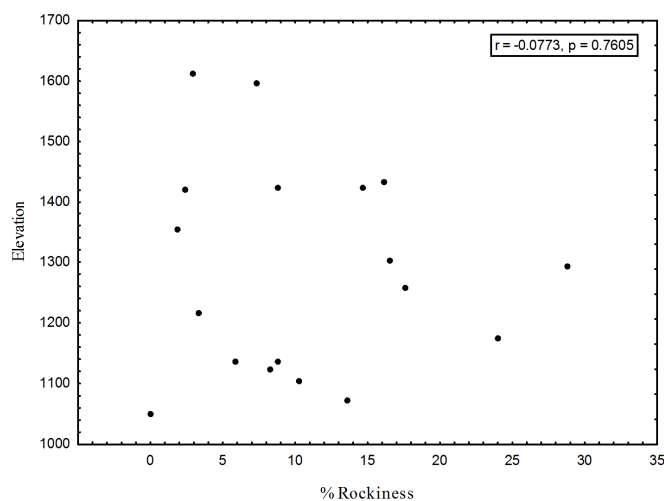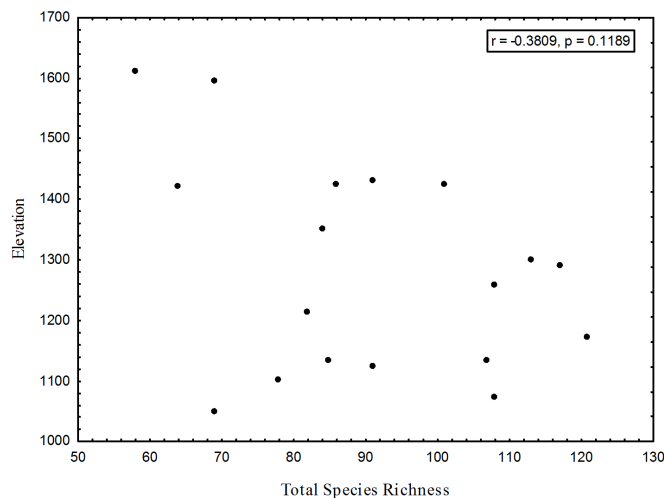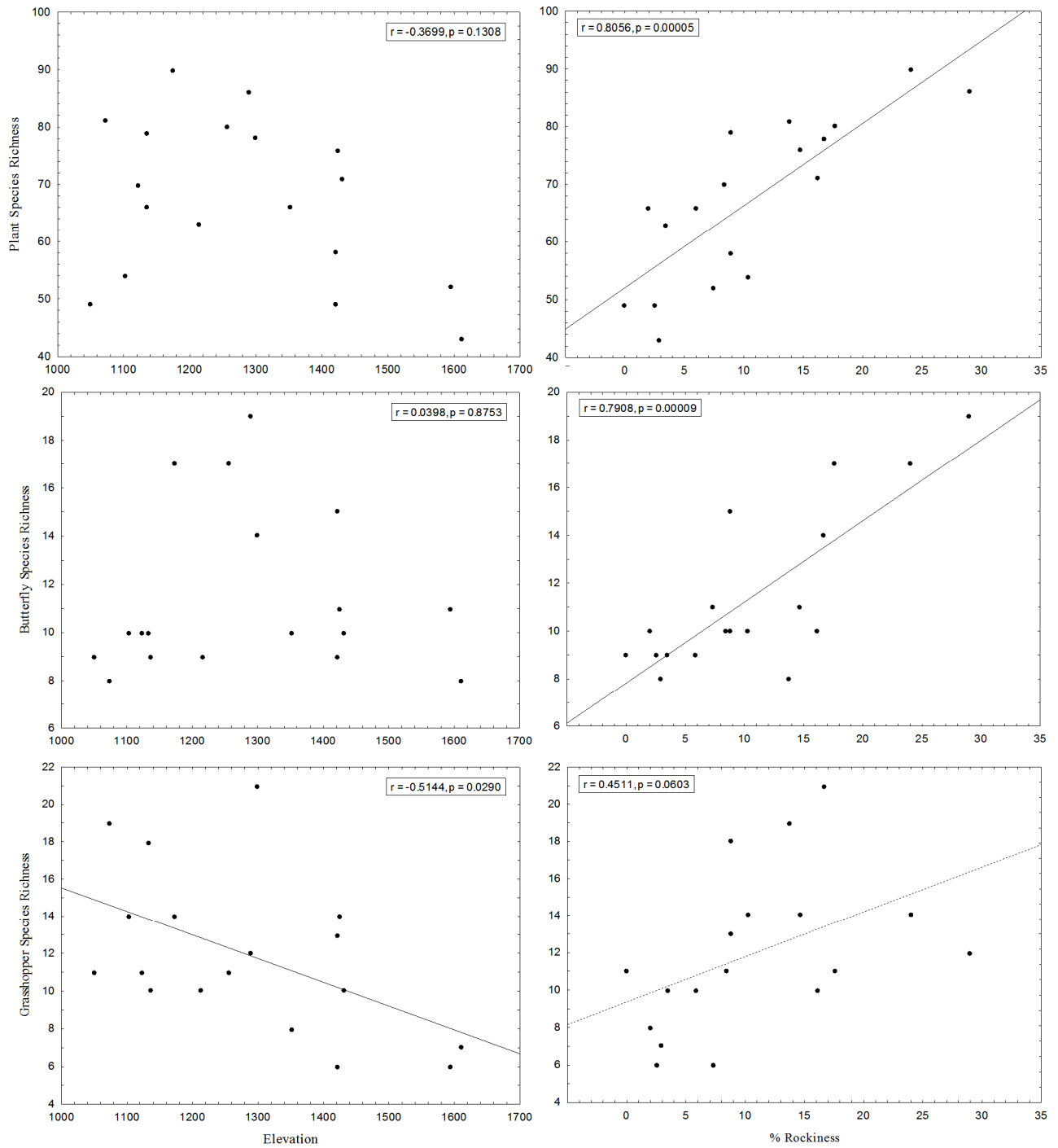
Figure 2.3 The relationships between plant, butterfly and grasshopper species richness, and elevation and % rockiness in a patch. n = 18

Furthermore, results from the generalised linear modelling (GLZ's) showed the significant influence of both percentage rockiness and elevation on the species richness of flora and grasshoppers (Table 2.1). However, for flora, percentage rockiness had a stronger

effect than elevation, whereas for grasshoppers the opposite was true. In contrast, percentage rockiness was the only variable which significantly influenced butterfly species richness (Table 2.1). Grasshopper abundance was significantly influenced by both elevation and percentage rockiness (Table 2.1). As with species richness, butterfly abundance was only significantly influenced by percentage rockiness (Table 2.1). None of the two tested variables significantly influenced floral abundance.

Table 2.1 Generalized linear modelling (GLZ) for species richness and abundance of taxa, showing their relationship with measured environmental variables

Taxon	Variable	*df*	Wald Statistic	*P*-value
Species Richness				
Flora	Elevation	1	6.70	**0.010**
	% Rockiness	1	42.74	**<0.001**
Butterflies	Elevation	1	0.20	0.659
	% Rockiness	1	10.81	**0.001**
Grasshoppers	Elevation	1	7.37	**0.007**
	% Rockiness	1	5.42	**0.020**
Abundance				
Flora	Elevation	1	2.11	0.146
	% Rockiness	1	2.62	0.106
Butterflies	Elevation	1	0.04	0.841
	% Rockiness	1	69.78	**<0.001**
Grasshoppers	Elevation	1	46.24	**<0.001**
	% Rockiness	1	29.90	**<0.001**

Values in bold are significant at the 5% level.

For flora, mean species richness differed significantly between categories (Fig. 2.4a), and was mainly driven by the significant decrease in species richness observed for areas that

had <10% rockiness. In particular, the category 'high elevation with <10% rockiness (High<10)' had on average lower species richness than all other categories, and significantly lower species richness than both areas of higher percentage rockiness. This result for flora was the same for grasshoppers (Fig. 2.4b). In contrast, butterfly species richness did not differ significantly across any of the categories (Fig. 2.4b). However, butterfly species richness was on average the highest in areas with higher percentage rockiness.
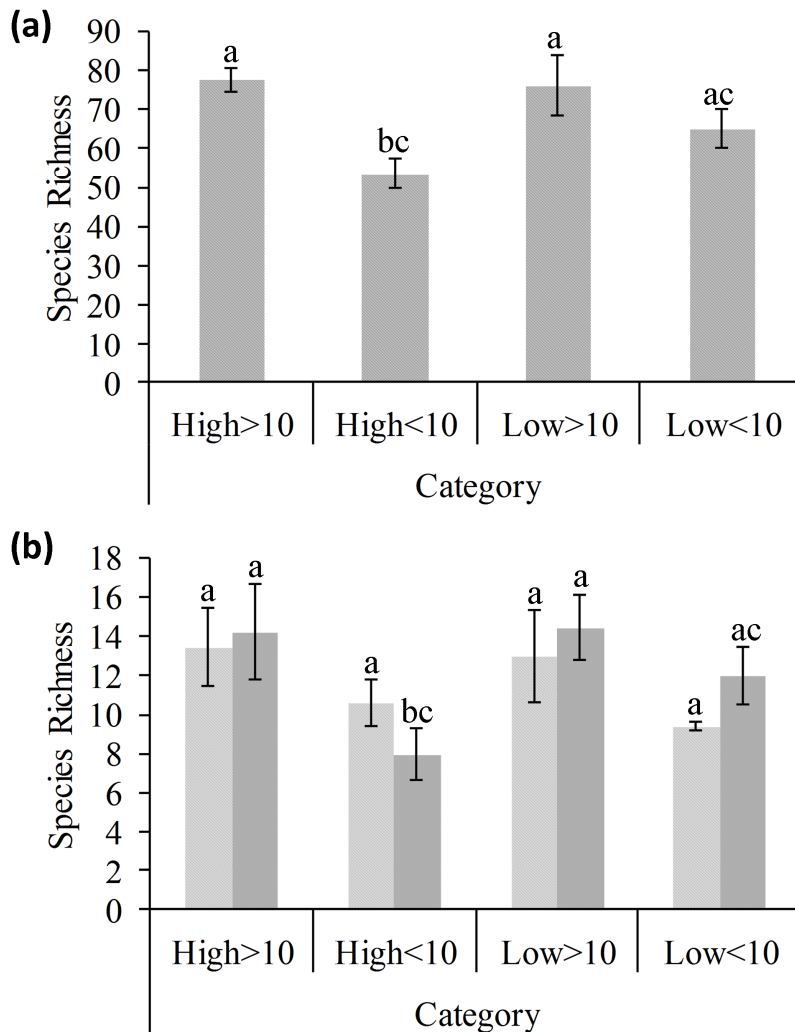
Figure 2.4 Mean (±SE) for (a) flora and (b) butterflies (light grey) and grasshoppers (dark grey) relative to measured environmental variables. High represents sites >1 280 m a.s.l., and low <1 280 m a.s.l. >10 represents areas that are greater than 10% rocky, and <10 areas lower than 10% rocky. Within taxa, means with different alphabetical letters differ significantly (P <0.05).

Table 2.2 Permutational multivariate analysis of variance (PERMANOVA) results on the effect of elevation and percentage rockiness per habitat on species composition for three taxa

	Taxon		
Factor	Flora	Butterflies	Grasshoppers
Overall Test	*P-value*	*P-value*	*P-value*
Rockiness	0.0532	**0.0024**	0.1318
Elevation	**<0.001**	0.2822	**0.0101**
Rockiness x Elevation	0.1359	0.8201	0.3157
Pairwise Test	*P-value*	*P-value*	*P-value*
>10High, <10High	**0.008**	0.3253	0.1089
>10High, <10Low	0.5612	**0.0073**	0.2533
>10High, >10Low	0.8257	0.8554	0.1715
<10High, <10Low	**0.0084**	0.295	**0.0338**
<10High, >10Low	**0.0068**	0.2922	**0.0168**
<10Low, >10Low	0.8099	**0.0082**	0.4635

High represents sites >1 280 m a.s.l., and low <1 280 m a.s.l. >10 represents areas that were >10% rocky, and <10 areas <10% rocky.

Values in bold are significant at the 5% level.

Species composition relative to measured environmental variables

Canonical correspondence analyses (CCA) revealed that assemblages of both flora and grasshoppers were more strongly structured in space by elevation than by percentage rockiness ($P = 0.004$ and $P = 0.287$, respectively) (Fig. 2.5a, c). In contrast, butterfly assemblage composition was more strongly influenced by percentage rockiness ($P = 0.089$) as opposed to elevation ($P = 0.256$) (Fig. 2.5b).

Similar to the CANOCO results, but with using our experimental categories, the only significant interaction between percentage rockiness and focal taxa composition was for butterflies (PERMANOVA, $P = 0.002$; Table 2.2). In turn, flora and grasshoppers were the only taxa which showed significant differences in assemblages relative to elevation (PERMANOVA, $P = <0.001$ and $P = 0.010$ respectively; Table 2.2). Pairwise tests showed that for flora, the combined group of high elevation sites with <10% rockiness was consistently driving the differences in species composition across sites (Table 2.2). Similar results were obtained for grasshoppers, although this result was not as pronounced as that of

flora. In contrast, the butterfly assemblage was not at all influenced by this combination of environmental variables. Instead, they were more strongly influenced by lower elevation areas with <10% rockiness (Table 2.2).
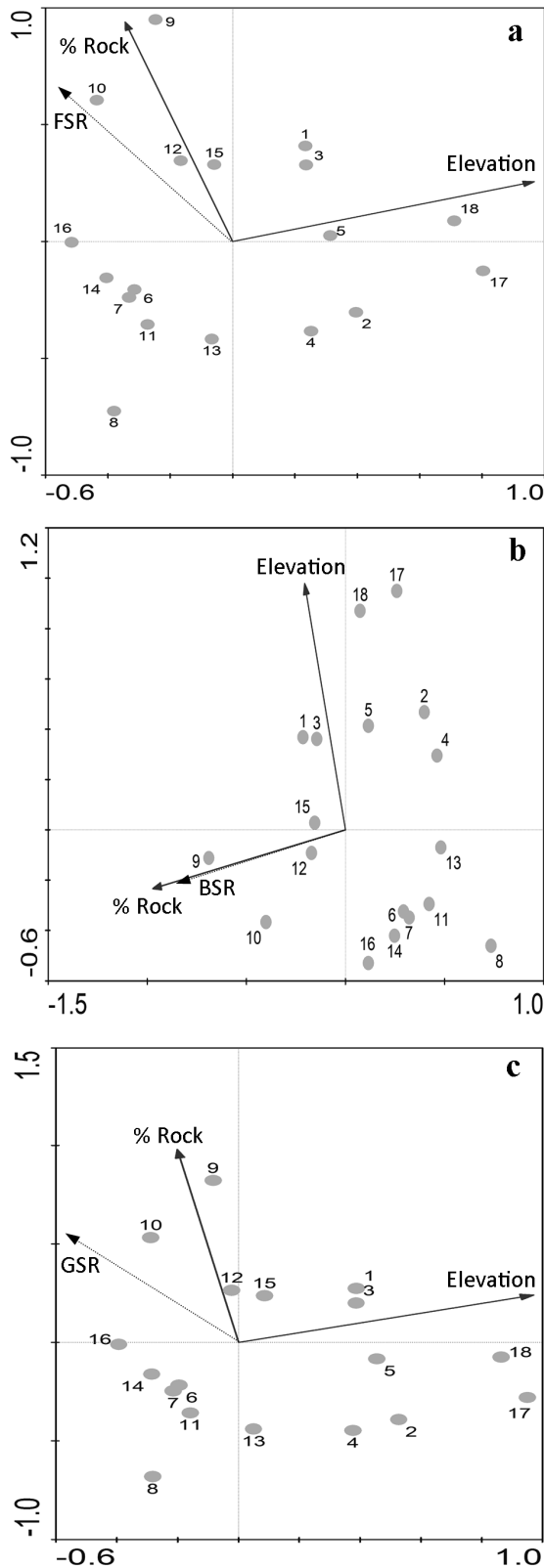
Figure 2.5 Canonical correspondence analysis (CCA) for (a) flora, (b) butterflies and (c) grasshoppers across sites, the two measured environmental variables, and a descriptive supplementary variable. Forward selection results showed that for flora, elevation had was a more significant influence than % rockiness (Elevation, P = 0.004; % Rock, P = 0.287); for butterflies, % rockiness was a stronger influence that elevation (Elevation, P = 0.256; % Rock, P = 0.089); and for grasshoppers, elevation was more significant than percentage rockiness (Elevation, P = 0.001; % Rock, P = 0.881). FSR, floral species richness; BSR, butterfly species richness; GSR, grasshopper species richness.

Discussion

Since the inception of the mesofilter concept (Hunter 2005), little research has been done to explore this as a practical field tool. Moreover, little has been done to explore the relationship between physical ecosystem features and species richness and composition for practical conservation planning. Here, I tested the use of rockiness as a mesofilter as described by Hunter (2005). This physical landscape feature had significant interactions in species richness and composition with all three focal taxa. This interaction illustrates how we can apply environmental data using a mesofilter to help optimize design of conservation plans, and thus management of biodiversity, at a landscape scale.

Overall, the percentage of rockiness is an important driver of the variation observed here for species richness across all studied taxa. This result was true whether using either continuous data or our experimental categories. In fact, using a specific delineation of higher or lower than 10% rockiness, it was sites with <10% rockiness where all taxa had lower species richness. Moreover, it is clear that plant and grasshopper species richness were also influenced by elevation. We could thus infer that rockiness and elevation are important variables in delineating biodiversity hotspots for plant and grasshoppers. However, species richness alone is a poor indicator of biodiversity as a whole (Purvis & Hector, 2000). For example, if one area had ten species and another had twenty, by using only species richness one might argue that the area with twenty species is more important to conservation. However, if the ten species found in the other site were significantly dissimilar in composition to the other area, both areas are indeed important for biodiversity conservation. In that sense, I also measured similarity/dissimilarity in species composition, and whether this difference could be a function of the rockiness/elevation mesofilter, and what this would mean for biodiversity planning. Both flora and grasshoppers showed significantly different species composition for elevation, but not rockiness. Specifically, for both taxa, it was the combination of >1 280 m a.s.l. and <10% habitat rockiness which influenced this observed assemblage difference. Essentially, for flora and grasshoppers at a landscape scale, we can more readily predict biodiversity 'micro-hotspots' (Grant & Samways 2011) as the rockiness mesofilter was strong enough to delineate biodiversity hotspots across two taxa. Furthermore, these results also emphasise the significance of both rockiness and elevation as mesofilters for delineating areas of conservation concern for plants and grasshoppers within this montane landscape.

The real question underlying these results is why these taxa would respond to the rocky mesofilter. Within grasslands, variable levels of fire disturbance are known to structure plant communities (Bond & Keeley 2005). Rocks within a landscape are implicated in lessening the severity of fires, and are thus creating refugia for certain fire sensitive species (Signell & Abrams 2006). Furthermore, rocks may also provide barriers against ground-dwelling herbivores that eat bulbous plants, again promoting the longevity of certain plants in rocky landscapes (Thomson *et al*. 1996). In grasshoppers, rocks are important structures that aid in thermoregulatory processes (Chappell 1983). Essentially, processes such as fire, predation, and thermoregulation, which occur across many ecosystems, could all be seen as confounding variables in the response of taxa to rockiness. However, since this was not explicitly tested here, it remains to be fully explored for this grassland landscape.

Interestingly, in this montane landscape, elevation had no significant influence on butterfly species richness. Grill *et al*. (2005) also found moderate elevation differences to have no relationship with butterfly species richness, and suggested that increased butterfly richness is in response to variation in favourable floral composition and structure. In contrast, variation in butterfly species richness has been shown to be a function of elevation and topographical heterogeneity (Mac Nally *et al*. 2003; Gutiérrez Illán *et al*. 2010). Overall, it seems that the factors influencing butterfly species richness might be a complex interaction between land cover heterogeneity, climate and topography (Kerr *et al*. 2001; Gutiérrez Illán *et al*. 2010). This means that diversity in land cover (measured at the large spatial scale) influences species composition in space, owing to different species inherently being associated with specific conditions (Fleishman *et al*. 2001). This would then ultimately explain the variation in species richness when measured at a small scale (Kerr *et al*. 2001). Consequently, butterfly species richness is a weak measure for delineating biodiversity hotspots at a small spatial scale, owing to high species turnover across a heterogeneous landscape.

The result from the butterfly PERMANOVA analysis supports the view that species richness alone is not an accurate indicator of biodiversity as a whole when measured at a small spatial scale. Percentage rockiness showed a strong influence in structuring dissimilar butterfly assemblages across this space. Thus, butterfly biodiversity micro-hotspots could not be predicted using the mesofilter. Nevertheless, this approach predicted whether a certain butterfly species is present or not. In other words, a certain assemblage of butterflies would be strongly associated with rocks, while another assemblage would be absent from such areas.

The reason for this behaviour in butterflies remains to be fully explored. Still, this result has important conservation planning implications at the spatial scale of the landscape, as changes in species composition for butterflies are strongly influenced by rockiness (see Hewitt *et al*. 2005). This then enables a planning approach where certain landscape features and characteristics, as preferred by different taxa, could be incorporated into the systematic conservation planning process (Margules & Pressey 2000; Lindenmayer *et al*. 2008).

Subsequently, the biotic surrogacy issues, as raised by Lindenmayer *et al*. (2002) and Ferrier (2002), could also be addressed through using this rocky mesofilter. Here the focus was on using abiotic surrogates. Lindenmayer *et al*. (2002) argued the probable failure of a focal species approach towards surrogacy, as habitat conditions are mostly variable and therefore species-specific requirements may also vary. Here, I kept the focal mesofilter constant. When more than one taxon is significantly associated with this mesofilter across space, whether through species richness or composition, as I show here, conservation planners can be more precise in knowing that species-specific requirements are kept constant across an area.

A further point is the importance of developing conservation planning tools, such as surrogates, which are likely to persist across different management regimes or environmental conditions (Hunter *et al*. 1988; Sarkar *et al*. 2006). In other words, surrogates need to be robust and designed so that they are consistently associated with their target species or taxa irrespective of habitat conditions due to varied management (e.g. between protected areas and unprotected remnant patches). Armstrong *et al*. (1994), studying natural habitats, showed that plant species richness within montane grasslands in South Africa was higher in rocky areas. I have also provided significant evidence for this also being the case in semi-natural montane grassland remnants. In essence, the mesofilter concept, as proposed through this rockiness proxy, fits this recommendation for more accurate surrogates (Sarkar *et al*. 2006). Moreover, rocks are physical ecosystem features that persist over long periods, despite climate change, again emphasising the mesofilter concept as a novel complementary approach to modern conservation planning (*sensu* Hunter *et al*. 1988). This highlights the value of a rockiness mesofilter as a conservation tool for this critically endangered habitat type in South Africa, and would likely have similar value if explored elsewhere.

An important question remaining is whether abiotic factors are generally important to conservation. The mesofilters of rockiness and elevation studied here suggest that it is, but are not the 'be all and end all' for conservation planning, as many other features might also exist

within a landscape, which would be as valuable to take into account. For example, different soil types were shown to be an important abiotic variable to take into account for conservation planning in prairie ecosystems in the United States (Wilsey *et al.* 2005). Similarly, logs in Yellow Box-Red Gum grassy woodlands in Australia were shown to have high beetle diversity, which was particularly important towards conservation planning for this taxon (Barton *et al.* 2009). The importance of abiotic variables in an aquatic environment has also been reported, where piles of shell debris can significantly enhance diversity (Hewitt *et al.* 2005). Soil type, logs and shell debris are therefore mesofilters within their respective landscapes. Essentially, any ecosystem can be thought of theoretically having many attributes or features that would be of conservation interest, and mesofilters are therefore a way of expressing this attribute to be used in wildlife conservation evaluation (Usher 1986). A particular mesofilter we delineate is therefore an important departure point from which we start conservation planning within a landscape in a rapidly changing environment.

Conclusion

There is an increasing need to understand the determinants of observed spatial heterogeneity in species richness and composition (whether at a large or small spatial scales), as this will greatly optimize conservation planning for both biodiversity maintenance and the movement of species under a changing climate (Gaston 2000). This study presents a mesofilter approach which adds to our current understanding of species distribution pertaining to certain landscape elements across a small spatial scale. Ultimately, the novelty arose by using an abiotic indicator approach, based on landscape elements that are easy to quantify and map and which are associated with multiple taxa. This would ease land-use decision making in similar areas where species inventories are currently lacking, and development is taking place rapidly (Carroll 1998; Fleishman *et al.* 2001; Mac Nally *et al.* 2003). I strongly argue the value and relevance of this mesofilter operational scale to be used alongside currently implemented conservation planning operational scales such as fine- and coarse-filter approaches (*sensu* Hunter 2005; Schulte *et al.* 2006).

References

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46

Armstrong, A.J. & van Hensbergen, H.J. (1999) Identification of priority regions for animal conservation in afforestable montane grasslands of the northern Eastern Cape Province, South Africa. *Biological Conservation*, **87**, 93-103

Armstrong, A.J., van Hensbergen, H.J. & Geertsema, H. (1994) Evaluation of afforestable montane grasslands for wildlife conservation in the north-eastern Cape, South Africa. Part 1. Methods. *South African Forestry Journal*, **171**, 7-20

Barton, P.S., Manning, A.D., Gibb H., Lindenmayer, D.B. & Cunningham, S.A. (2009) Conserving ground-dwelling beetles in an endangered woodland community: multi-scale habitat effects on assemblage diversity. *Biological Conservation*, **142**, 1701-1709

Bieringer, G. & Zulka, K.P. (2003) Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. *Biodiversity and Conservation*, **12**, 1481-1495

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution, **20**, 387-394

Carroll, S.S. (1998) Modelling abiotic indicators when obtaining spatial predictions of species richness. *Environmental and Ecological Statistics*, **5**, 257-276

Chappell, M.A. (1983) Thermal limitations to escape responses in desert grasshoppers. *Animal Behaviour*, **31**, 1088-1093

Everson, C.S. & Clarke, G.P.Y. (1987) A comparison of six methods of botanical analysis in the montane grasslands of Natal. *Vegetatio*, **73**, 47-51

Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology*, **51**, 331-363

Fleishman, E., Mac Nally, R., Fay, J.P. & Murphy, D.D. (2001) Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. *Conservation Biology*, **15**, 1674-1685

Gardiner, T., Hill, J. & Chesmore, D. (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *Journal of Insect Conservation*, **9**, 151-173

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391

Grant, P.B.C. & Samways, M.J. (2011) Micro-hotspot determination and buffer zone value for Odonata in a globally significant biosphere reserve. *Biological Conservation*, **144**, 772-781

Grill, A., Knoflach, B., Cleary, D.F.R. & Kati, V. (2005) Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. *Biodiversity and Conservation*, **14**, 1281-1300

Gutiérrez Illán, J., Gutiérrez, D. & Wilson R.J. (2010) Fine-scale determinants of butterfly species richness and composition in a mountain region. *Journal of Biogeography*, **37**, 1706-1720

Hayes, G.F. & Holl, K.D. (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology*, **17**, 1694-1702

Hewitt, J.E., Thrush, S.E., Halliday, J. & Duffy, C. (2005) The importance of small-scale habitat structure for maintaining beta-diversity. *Ecology*, **86**, 1619-1626

Hunter Jr., M.L. (2005) A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology*, **19**, 1025-1029

Hunter Jr., M.L., Jacobsen Jr., G.L. & Webb III, T. (1988) Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology*, **2**, 375-385

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences USA*, **98**, 11365-11371

Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I. & McCarthy, M.A. (2002) The focal-species approach and landscape restoration: a critique. *Conservation Biology*, **16**, 338-345

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Cullen, P., Driscoll, D., Fahrig, L., Fisher, J., Franklin, J., Haila, Y., Hunter, M., Gibbons, P., Lake, S., Luck, G., MacGregor, C., McIntyre, S., MacNally, R., Manning, A., Miller, J., Mooney, H., Noss, R., Possingham, H., Saunders, D., Schmiegelow, F., Scott, M., Simberloff, D., Sisk, T., Tabor, G., Walker, B., Wiens, J., Woinarski, J. & Zavaleta, E. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters*, **11**, 78-91

Mac Nally, R., Fleishman, E., Fay, J.P. & Murphy, D.D. (2003) Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. *Biological Conservation*, **110**, 21-31

Maiorano, L., Falcucci, A. & Boitani. L. (2008) Size-dependant resistance of protected areas to land-use change. *Proceedings of the Royal Society B*, **275**, 1297-1304

Marcot, B.G. & Flather, C.H. (2007) Species-level strategies for conserving rare or little-known species. *Conservation of rare or little-known species: biological, social and economic considerations* (eds. M.G. Raphael & R. Molina), pp. 124-164. Island Press, Washington DC, USA

Margules, C.R., Nichous, A.O. & Pressey, R.L. (1988) Selecting networks of reserves to maximise biological diversity. *Biological Conservation*, **43**, 63-76

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243-253

McCulloh, C.E., Searle, S.R. & Neuhaus, J.M. (2008) *Generalized, linear, and mixed models*, 2nd edition. Wiley, USA

McNatty, A., Abbott, K.L. & Lester, P.J. (2009) Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands. *Oecologia*, **160**, 187-194

Mucina, L. & Rutherford, M.C. (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria

Noss, R. (1987) From plant communities to landscape in conservation inventories: a look at the Nature Conservancy (USA). *Biological Conservation*, **41**, 11-37

Noss, R.F., Carroll, C., Vance-Borland, K. & Wuerthner, G. (2002) A Multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone ecosystem. *Conservation Biology*, **16**, 895-908

Overton, C.T., Casazza, M.L. & Coates, P.S. (2010) Scale association of Band tailed pigeon counts at mineral sites. *Northwestern Naturalist*, **91**, 299-308

Overton, C.T., Schmitz, R.A. & Casazza, M.L. (2006) Linking landscape characteristics to mineral site use by Band-Tailed Pigeons in Western Oregon: coarse-filter conservation with fine-filter tuning. *Natural Areas Journal*, **26**, 38-46

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in Ecology and Evolution*, **22**, 583-592

PRIMER-E. 2008. PERMANOVA and PRIMER 6. PRIMER-E, Lutton

Pryke, J.S. & Samways, M.J. (2012). Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology*, **27**, 73-85

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, **405**, 212-219

Rich, T., Rebane, M., Fasham, M., McGeechan, F. & Dobson, D. (2005) Methods for surveying habitats: ground and shrub vegetation. *Handbook of Biodiversity Methods: survey, evaluation and monitoring* (eds. D. Hill, M. Fasham, G. Tucker, M. Shewry & P. Shaw), pp. 201-221. Cambridge University Press, Cambridge, UK

Samways, M.J. & Moore, S.D. (1991) Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation*, **57**, 117-137

Samways, M.J., McGeoch, M.A. & New, T.R. (2010) *Insect Conservation: a handbook of approaches and methods*, 1st edition. Oxford University Press, Oxford, UK

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S. (2006) Biodiversity conservation planning tools: present status and challenges for the future. *Annual Reviews on Environment and Resources*, **31**, 123-159

Schulte, L.A., Mitchell, R.J., Hunter Jr., M.L., Franklin, J.F., McIntyre, R.K. & Palik, B.J. (2006) Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S. *Forest Ecology and Management*, **232**, 1-11

Schwartz, M.W. (1999) Choosing the appropriate scale of reserves for conservation. *Annual Review of Ecology and Systematics*, **30**, 83-108

Signell, S.A. & Abrams, M.D. (2006) Influence of rocky landscape features and fire regime on vegetation dynamics in Appalachian *Quercus* forests. *Journal of Vegetation Science*, **17**, 675-684

Stohlgren, T.J. & Bachand, R.R. (1997) Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology*, **78**, 632-641

ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO reference manual and user's guide to Canoco for windows: software for Canonical community ordination (version 4.5).* Microcomputer Power, Ithaca

Thomson, J.D., Weiblin, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698-1715

Tucker, G., Fasham, M., Hill, D., Shewry, M., Shaw, P. & Wade, M. (2005) Planning a

programme. *Handbook of Biodiversity Methods: survey, evaluation and monitoring* (eds. D. Hill, M. Fasham, G. Tucker, M. Shewry & P. Shaw), pp. 6-64. Cambridge University Press, Cambridge, UK

Usher, M.B. (1986) Wildlife conservation evaluation: attributes, criteria and values. *Wildlife Conservation Evaluation* (ed. M.B. Usher), pp. 3-44. Chapman and Hall, London

Van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S., Hull, H., Bellamy, C., Krueger, M., Endroedy-Younga, S., Mansell M.W. & Scholtz C.H. (1998). Biodiversity assessment and conservation strategies. *Science*, **279**, 2106-2108

Wessels, K.J., Freitag, A.S. & van Jaarsveld, A.S. (1999) The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biological Conservation*, **89**, 21-38

Whalley, R.D.B. & Hardy, M.B. (2000) Measuring Botanical Composition of Grasslands. *Field and Laboratory Methods for Grassland and Animal Production Research* (eds. L. 't Mannetje & R.M., Jones), pp. 67-102. CABI Publishing, UK

Wilsey, B.J., Martin, L.M. & Polley, H.W. (2005) Predicting plant extinction based on species-area curves in prairie fragments with high beta richness. *Conservation Biology*, **19**, 1835-1841

Chapter 3

Associations between plant growth forms and rockiness explain plant diversity across a grassland landscape

Abstract

A complex set of variables may explain biodiversity patterns both locally and regionally. Evidence exist that greater plant species richness can be associated with localized areas containing a greater percentage of rock exposure. Here, I test whether this is the case at the landscape scale, using semi-natural montane grassland in southern Africa. Plants were inventoried, and percentage rock exposure calculated, and each site graded according to three levels of rockiness. Soil samples from each site were then analysed for particle size, as well as for levels of carbon, nitrogen, and available phosphorus. Species richness and the compositional similarity of assemblages were compared between the three rockiness categories. Plants were then categorised into their respective growth forms, and species richness within each group also compared across the rockiness categories. Greater species richness in rockier landscapes was driven by two particular plant growth forms, geophytes and perennial grasses. However, no overall plant assemblage compositional changes were recorded between the various rockiness categories, indicating that only very few species are not associated with rocky areas in some way in this landscape. This shows that plant species within certain life-form groups are naturally more responsive to certain abiotic ecosystem elements than others across a landscape. In turn, this highlights the significance of high habitat heterogeneity in structuring plant communities. Consequently, when an abiotic feature such as rockiness is observed across a landscape, it provides a surrogate for the spatial heterogeneity of certain plant communities.

Introduction

Distribution patterns of species are typically influenced by eco-physiological constraints, environmental disturbances such as droughts or habitat fragmentation, and resources such as nutrients (reviewed in Guisan & Thuiller 2005). In turn, abiotic factors often have a great influence on community dynamics, including species abundance, as opposed to compensatory interactions such as competition (Houlahan *et al*. 2007). However, competitive exclusion within communities is a major principle for explaining why some areas naturally display higher species richness than others (Palmer 1994). The competitive exclusion principle suggests that greater competition within a community would mostly lead to lower species richness. Theoretically then, at a smaller spatial scale, areas of higher species richness could therefore indicate higher habitat heterogeneity, as variable microsite conditions often exhibit more complex resource differentiation and specialization (Auerbach & Shmida 1987). For example, there is an important positive relationship between plant species richness and variable environmental conditions at the local or meso-scale (tens to hundreds of meters) (Bruun *et al*. 2003; Dufour *et al*. 2006). This highlights the use of environmental predictors at a landscape scale to describe biodiversity patterns, and could be of value in wildlife conservation evaluation.

Greater percentage rockiness (i.e. exposed rock surface rather than soil covered rock), can be associated with higher plant species richness in montane grasslands (Chapter 2). Furthermore, higher abundance of geophytic orchids is also linked to more rocky patches within grassland habitats (Landi *et al*. 2009). However, the reason why more plant species are specifically associated with high levels of rockiness still remains to be explained. Certainly, rocky habitats influence vegetation patterns by providing habitats with less moisture availability (rendering plants more adapted to physiologically drier conditions), through fire protection (Kirkpatrick *et al*. 1988), and through greater structural complexity of the landscape (greater microhabitat heterogeneity) (Lambrinos *et al*. 2006). In essence, there seems to be a strong link between physical habitat elements, specialised plant growth forms, and plant biodiversity patterns across the landscape.

In addition, soil nutrient levels of elements such as carbon and nitrogen explain variable levels of species richness among grassland vegetation, in addition to rockiness (Maccherini 2006), indicating a probable link between rockiness and nutrients. Available phosphorus in soils also influences the proportion of plant growth forms (Durrough &

Scroggie 2008). There is also evidence that patterns in grassland species richness could be explained by differences in soil types (a measure of habitat heterogeneity) (Bruun 2000).

In view of insufficient information explaining why higher plant species richness is associated with higher rockiness, I investigate here the reasons for this in a montane grassland landscape, specifically at the meso-scale. By controlling for elevation (*sensu* Chapter 2, Fig. 2.4a, where sites in category High<10 were removed), I explore whether species distribution variation at this scale is an artefact of the inherent, indirect, ecological association of different specialist plant growth forms to heterogeneous microsite conditions, as generated by variable levels of rockiness (*sensu* Auerbach & Shmida 1987; Thomson *et al*. 1997; Lambrinos *et al*. 2006). I also determine whether there exist edaphic correlates of rockier patches at the meso-scale, such as soil texture (soil hydraulic characteristics) and soil nutrients, and whether such relationships can help explain the rockiness-plant diversity interaction. By addressing these issues, we can view the landscape not simply as a random assortment of species, but as a way of understanding the role of certain functional groups and their abiotic correlates in structuring plant biodiversity patterns (Purvis & Hector 2000).

Methods

Study area

The study was undertaken within the 16 000 ha Merensky Forestry estate at Weza, near Kokstad, KwaZulu-Natal, South Africa (S 30°34.855, E 029°44.726). Around 4 200 ha semi-natural open spaces are on the estate, the remainder being commercial plantation forestry. These remnants are classified mostly in the endangered Midlands Mistbelt Grassland vegetation type (Mucina and Rutherford 2006). The endangered status of this vegetation type is driven mainly by the threat of landscape transformation by forestry plantations in the area. These grasslands are dominated by the grass *Themeda triandra* Forssk. All selected sites were classified as semi-natural, as all were annually burned by forestry management for >6 decades. Moreover, grazing is minimal within these remnants, and consequently fire is the main 'herbivore' in this landscape (Bond & Keeley 2005). All sampling was done >30 m away from the commercial plantation edge so as to reduce sampling bias due to edge effects (Bieringer & Zulka 2003; Pryke & Samways 2012).

The geology is sand and siltstones from the Ecca group. Weathered resistant dolerite dykes are also present. The maximum height of the mountains is 2 200 m a.s.l., above an undulating landscape with minimum elevation of 900 m a.s.l. This is a summer rainfall region, where most precipitation is between November and March. Annual precipitation varies ~1000 mm per annum in the low lying areas, to 1500 mm on the mountain peaks. Mean daily maximum temperature ranges from 17.6˚C in June to 26˚C in January. Mean daily minimum temperature range from 0.1˚C in June to 13.4˚C in January.

Vegetation sampling

Thirteen vegetation sampling sites were selected within the remnant semi-natural open spaces (*sensu* Chapter 2 (elevation effect), sites 2, 4, 5, 17 and 18 were excluded; see Fig. 2.1 & 2.4a). Sampling was between January and February 2011 through a fixed grid sampling design, where sampling is taken at fixed intervals along a determined gradient (Whalley & Hardy 2000). This sampling method is relatively easy to perform in the field, and leads to rapid yet accurate acquisition of data on species distribution and abundance within a study area (Tucker *et al*. 2005). Within this design, I used point intercept line transects, as this method has been shown to be relevant and insightful for biodiversity studies in these grasslands (Everson & Clarke 1987; Armstrong *et al*. 1994).

Field methods were similar to Hayes and Holl (2003), where a measuring tape, 50 m long, was used to record all plant species that intercept a 1.8 mm-diameter pin every 1 m (51 points per transect). For grasslands, a dense vegetation type, transects of 50 m are seen as adequate (Rich *et al*. 2005). A total of four 50 m transects were placed within each of the thirteen sites, each transect being 15 m away from another, effectively having 204 points per site. Percentage rockiness was measured in two ways: 1) when rocks were touched by the pin, they were added and then divided by the total number of hits (204) and a percentage rockiness was then calculated; 2) a metal stake was inserted in the ground every 5 m on each transect, giving 40 measurements per site, which serves as a composite indicator of surface rockiness (Stohlgren & Bachand 1997). This ensured correct classification of the landscape as rocky, and not just a rocky outcrop within a non-rocky matrix. In addition, a one meter belt, perpendicular to the line transect, was time-searched (15 min) after each transect measurement, as a means for recording a more comprehensive species list that could include short lived annual plants (Hayes & Holl 2003).

To avoid pseudoreplication, sites of higher rockiness were interspersed with those of intermediate and lower rockiness across the study area, with the minimum distance between similar sites being 400 m.

Soil analysis

At each site, 10 soil samples (+/- 100 g each) were taken, diagonally across each site, at ~5-10 cm depth, and then bulked. Bulked samples were air dried until a constant weight was achieved, and passed through a 2 mm sieve. Samples were analysed for soil texture (sand, silt and clay particle sizes) according to the pipette method (Gee & Baulder 1986). Plant available phosphorus content was determined using the Bray 2 extraction method (Kuo 1996). Carbon and nitrogen content was calculated by dry combustion using a EuroVector Elemental Analyzer.

Statistical analysis

All plant species (n = 210) were classified into six growth forms: Annual Graminoids (Poaceae and Cyperaceae), Perennial Graminoids (Poaceae and Cyperaceae), Annual Forbs (herbaceous dicots), Perennial Forbs, Geophytes (herbaceous monocots), and Shrubs (woody dicots) (classifications as per Durrough & Scroggie 2008). Ferns are also a separate growth form, but as only one fern species was recorded here, I omitted it from the analysis. The soil texture data were classified as percentage sand, silt and clay. Soil nutrients were percentage carbon (C) and nitrogen (N), and available phosphorus (P) (mg.kg^{-1}). The 13 sites were then classified in three rockiness categories: <8% rocky (n = 4), intermediate rockiness (8-16%) (n = 5), and >16% rocky (maximum of 29%) (n = 4). To justify this classification, rockiness values were tested for normality and their variances tested for homogeneity using a Shapiro-Wilk test (Statistica Release 10, StatSoft, Inc.). The points were normally distributed around the mean. Percentage rockiness was presented as a three-way classification to simulate a step-wise increase in rockiness as was measured across this landscape at the meso-scale.

To explore the relationship between soil edaphic variables, total species richness, and plant growth form species richness, a Spearman rank correlation table was constructed. Then, to explore the contribution of percentage rockiness and elevation on species richness and the significant plant growth form correlates of total species richness, I made use of generalized

linear models (GLZ) (McCulloch *et al.* 2008) in Statistica Release 10 (StatSoft, Inc.). Each GLZ had a normal distribution and an identity-link function.

All plant and soil categories were tested for normality and their variances tested for homogeneity using a Shapiro-Wilk test (Shapiro & Wilk 1965) (Statistica Release 10, StatSoft, Inc.). Data for nitrogen, annual graminoids and shrubs were not normally distributed, thus non-parametric Kruskall-Wallis one-way analysis of variance was performed (Statistica Release 10, StatSoft, Inc.). Significant differences between rockiness groups were calculated using pairwise multiple comparisons of means. For all other categories, a one-way analysis of variance (ANOVA) was used to compare species and growth form richness, soil classification, and nutrient groups across the rockiness categories. This was followed by a Fisher LSD post-hoc test to identify any pairwise differences between rockiness (Statistica Release 10, StatSoft, Inc.).

To explore whether differences in species composition across study sites (if any) could be a function of rockiness, I used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) in PRIMER 6 (PRIMER-E 2008). I used an overall test, comparing species composition across rockiness. In addition, PERMANOVA was used to determine compositional differences within plant growth forms which differed in species richness when compared across the rockiness index. PERMANOVA results are reported as *P*-values (e.g. McNatty *et al.* 2009), where a significant *P*-value then indicates a significant difference (at the 5% level) between levels (groups) of a studied factor. Analyses were performed using Bray-Curtis similarity measures where data for each group were fourth-root transformed to reduce the weight of the common species (Anderson 2001).

Results

Higher total species richness was shown to be a function of specifically three plant growth forms: perennial grass richness (r = 0.888, *P* < 0.05), geophyte richness (r = 0.738, *P* < 0.05), and shrub richness (r = 0.599, *P* < 0.05) (Table 3.1). Measured soil nutrients had no relationship with either total plant species richness or any plant growth form species richness specifically (Table 3.1). Soil texture classifications had no significant relationships with either total species richness or the significant plant growth form correlates of total species richness (Table 3.1).

Generalized linear modelling (GLZ) showed that percentage rockiness across a meso-scale has a highly significant influence on total species richness ($P < 0.001$), as well as on the two strongest plant growth form drivers of total species richness (perennial grass richness, $P < 0.001$; and geophyte richness, $P < 0.001$) (Table 3.2). In turn, elevation had no significant effect on either total species richness or the tested plant growth forms (Table 3.2).

Overall, species richness was significantly higher in the >16% rocky category than the <8% rocky category (Fig. 3.1, $P < 0.05$). Only two plant growth forms significantly differed across the rockiness classification, perennial grasses and geophytes (Fig. 3.1; see also Appendix D, E). Within each of these plant growth forms, there were significantly more species at the >16% rocky sites, as opposed to the <8% rocky sites, a similar result for overall species richness (Fig. 3.1, $P < 0.05$). In addition, within the geophyte group, the intermediate rocky sites (8-16% rocky) also significantly differed from the <8% rocky sites ($P < 0.05$).

Table 3.1 Spearman rank correlations (r – values) for all tested soil edaphic variables on growth form species richness as well as total species richness, as measured at the meso-scale.

	% Sand	% Silt	% Clay	P	N	C	AFR	PFR	AGR	PGR	GR	SR	TR
% Sand	1.000	0.423	**-0.599**	0.303	**0.696**	0.544	**0.565**	0.058	-0.136	0.300	0.499	0.104	0.440
% Silt		1.000	**-0.940**	0.479	0.514	**0.566**	0.457	**0.581**	-0.262	0.050	0.031	0.318	0.077
% Clay			1.000	**-0.577**	**-0.649**	**-0.665**	**-0.607**	-0.519	0.228	-0.008	-0.045	-0.245	-0.071
P				1.000	0.477	0.490	0.462	0.330	0.182	0.074	-0.182	0.189	0.028
N					1.000	**0.963**	0.493	0.074	0.275	0.163	0.485	-0.012	0.275
C						1.000	0.389	0.114	0.313	0.055	0.390	-0.070	0.143
AFR							1.000	0.373	-0.217	0.394	0.141	0.502	0.272
PFR								1.000	-0.264	0.447	-0.076	0.541	0.411
AGR									1.000	0.013	0.002	-0.461	-0.114
PGR										1.000	**0.557**	**0.656**	**0.888**
GR											1.000	0.200	**0.738**
SR												1.000	**0.599**
TR													1.000

P, phosphorus (mg.kg^{-1}); N, % nitrogen; C, % carbon; AFR, annual forb richness; PFR, perennial forb richness; AGR, annual grass richness; PGR, perennial grass richness; GR, geophyte richness; SR, shrub richness; TR, total richness

Values in bold are significant at the 5% level

Table 3.2 Generalized linear modelling of total species richness and its significant plant growth form correlates across percentage rockiness and elevation at the meso-scale.

	Variable	*df*	Wald Statistic	*P* - value
Total Species Richness	Elevation	1	0.095	0.758
	% Rockiness	1	20.702	**<0.001**
Perennial Grass Richness	Elevation	1	0.106	0.744
	% Rockiness	1	13.149	**<0.001**
Geophyte Richness	Elevation	1	0.410	0.522
	% Rockiness	1	27.401	**<0.001**
Shrub Richness	Elevation	1	0.953	0.328
	% Rockiness	1	1.780	0.182

Values in bold are significant at the 5% level
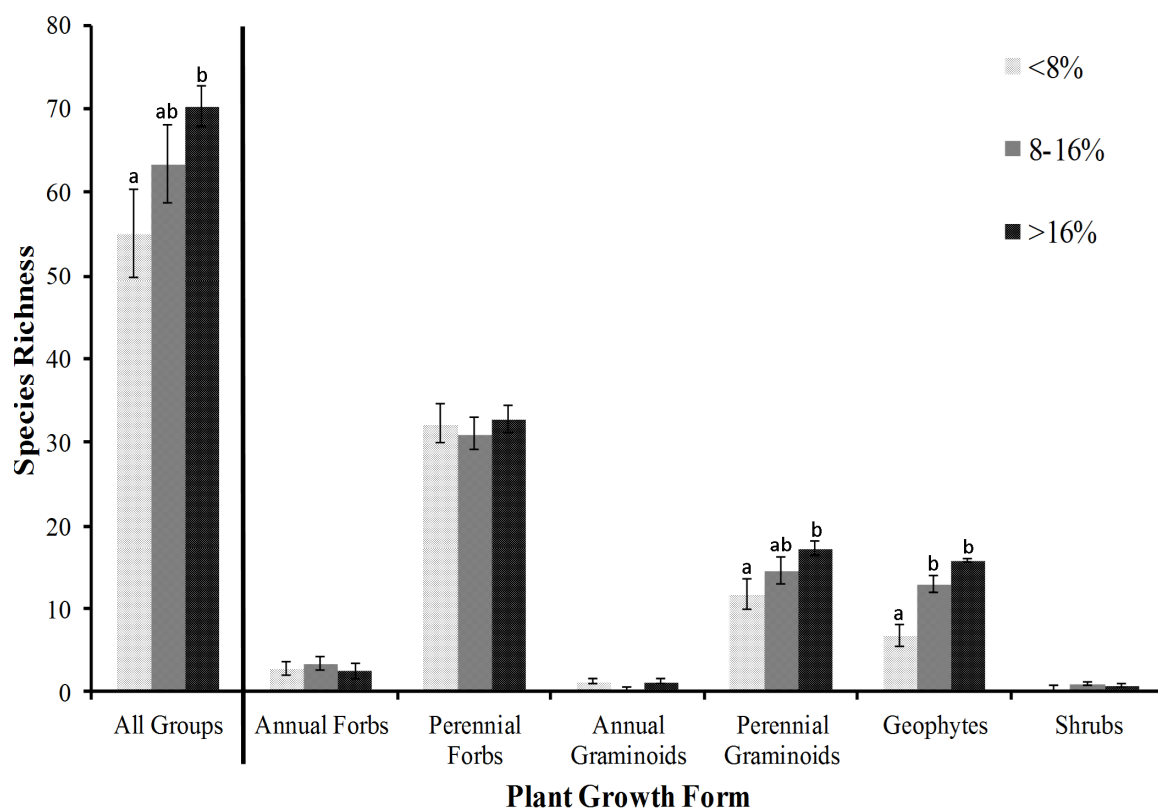
Figure 3.1 Mean species richness (± 1 SE) for all groups, and for each plant growth form individually, across three rockiness categories. For each growth form, means with different superscripts differ significantly.

Overall, there was no significant difference in species composition across all sites when tested against a rockiness factor (Table 3.3). This result was consistent with the perennial grass and geophyte plant growth form.

Table 3.3 PERMANOVA analyses of the influence of a three-way rockiness factor on plant species composition across all plant species recorded, across all sites, as well as for the two plant growth forms that were significantly different in species richness across the three way rockiness factor.

	df	**Pseudo-F**	*P* **- value**
Overall	2	1.33	0.065
Perennial Grass Richness	2	1.39	0.106
Geophyte Richness	2	1.01	0.454

Specified soil texture classifications did not differ significantly between rockiness categories (Table 3.4). Within the soil nutrients tested, available phosphorus (P) was the only element which differed across the tested rockiness categories, with the 8-16% rocky sites having significantly less available P than the <8% rocky sites.

Table 3.4 Means ($\pm$ 1 SE) for soil texture and nutrient classifications across a habitat rockiness index. Within each classification, means with different superscripts differ significantly.

Edaphic Factor	Classification	Rockiness Category		
		<8%	**8-16%**	**>16%**
Soil Texture	Sand (%)	15.57±6.15	17.69±2.42	19.59±1.03
	Silt (%)	53.1±8.39	49.29±4.27	50.31±3.43
	Clay (%)	31.33±10.94	33.02±6.58	30.1±3.12
Soil Nutrients	Phosphorus (mg.kg^{-1})	3.65±0.74[a]	1.64±0.44[b]	2.98±0.43[ab]
	Nitrogen (%)	0.33±0.04	0.36±0.06	0.37±0.01
	Carbon (%)	6.94±1.10	6.87±1.16	7.26±0.10

Discussion

A complex set of abiotic variables often explain local, spatial plant diversity patterns. Here, higher rockiness, and not elevation, was an accurate surrogate for higher montane grassland plant species richness across all sites. It was most pronounced when comparing the two most extreme categories of <8% and >16% rockiness. Furthermore, percentage rockiness is potentially a surrogate for many other abiotic as well as biotic variables.

High rockiness, or habitat 'structural heterogeneity', has been shown to positively relate to desert species richness (Montaña 1990). In South African montane grasslands, there are indications that rockier areas support higher plant species diversity (Armstrong *et al*. 1994; Chapter 2). However, in Argentinian montane grasslands, Cantero *et al*. (2003), using subjective classifications of rockiness, stoniness and soil depth, found no relationship between native species richness and rockiness. They did however, find a significant positive relationship for stoniness and a significant negative relationship for soil depth, the latter being a proxy for rockiness (Stohlgren & Bachand 1997). In contrast, a negative relationship between rockiness and species richness has also been demonstrated (Maccherini 2006). Here, the sampling spatial scale is important for explaining these inconsistencies in literature. Maccherini (2006), for example, studied a rockiness-species richness interaction at a small scale (0.25 m^2 plots), whereas here I focussed on a larger scale (200 m^2 plots), with the highest percentage rockiness measured being 29%. Low species richness in small plots, where a single rock could fill most of the area sampled, is logical. Subsequently, if rockiness is seen as an abiotic legacy (Turner & Dale 1998), this relationship between percentage rockiness and species richness is consistent with a curvilinear trend. This means that at certain spatial scales, there is likely to be low species richness associated with either low or high rockiness, while at intermediate rockiness species richness will peak. However, homogenous areas of only rock surface are less probable at a larger sampling unit size. This result is important for inferences pertaining to rockiness-plant interactions within an ecosystem. Overall, there seems to be an important measurable interaction between species presence/absence and levels of rockiness within a habitat.

Certain environmental factors can influence the species richness of certain plant growth forms (Montaña 1990). Specific plant growth forms are especially responsive, either positively or negatively, to certain abiotic factors (Dorrough & Scroggie 2008). Consistent with the relationship in overall species richness across the rockiness categories in our study,

were two particular growth forms: perennial grasses and geophytes. This result, where plant growth forms responded strongly to higher rockiness, is consistent with a study of Chilean montane plant species (Lambrinos *et al*. 2006), and seen as a result of the heterogeneous conditions created through rockiness within a landscape. Specifically, rocky areas are known to be strongly correlated with geophytes (Hadar *et al*. 1999). However, our results indicate that perennial grasses in addition to geophytes were driving the observed higher species richness in rockier areas of our grassland ecosystem.

There were no overall plant compositional changes between the studied sites, nor for either perennial grasses or geophytes alone. This is an important result, as it shows that there is little or no exclusion of any species when species richness becomes high as a result of high percentage rockiness. Also, this implies that the majority of species across this landscape (perennial forbs or herbaceous dicots) are generalists, occurring across many variable microhabitats, at least in relation to rockiness. Yet, there are specialist plant species, within specific growth forms, which are ecologically associated with rockiness, and this explains why rockiness determined the presence of local plant biodiversity hotspots at this landscape scale (see Appendix D, E). Indeed, communities that are geographically isolated, but environmentally similar (rockiness categories in this case), should have similar growth forms or species richness (Auerbach & Schmida 1987).

Essentially, habitat specialists occur within these montane grasslands, validating the concept that higher habitat heterogeneity, as a function of various abiotic legacies, often exhibits more complex resource differentiation and specialization, even at small spatial scales (Auerbach & Shmida 1987). Still, it is inadequate to advocate abiotic legacies *per se* as a cause for higher species diversity, without also suggesting how or why such a physical ecosystem feature is possibly influencing these plant diversity dispersion patterns (Roxburgh *et al*. 2004). In other words, what confounding variables might exist for varying levels of rock exposure in a landscape? This suggests that geophytes and perennial grasses hold the key to explaining these patterns.

Edaphic factors, such as moisture and nutrients, affect community composition in space (Frank & McNaughton 1991). Results from our study showed that none of the soil texture classifications, as a proxy for soil hydraulic characteristics (see English *et al*. 2005), changed with percentage rockiness. Likewise, soil nutrients across the three rockiness categories did not differ significantly, except for P in the 8-16% rocky category. Overall, therefore, these selected edaphic variables were not generally associated with the rockiness

categories at this meso-scale, while plant species richness was, and strongly so. As such, the observed species richness-rockiness interaction in this montane grassland ecosystem could not be explained through attributes of certain soil characteristics. This is in contrast to Maccherini (2006) who suggested carbon and nitrogen levels explain variable levels of species richness in grassland vegetation, in addition to rockiness. However, this study was at a much smaller spatial scale, and again emphasises the importance of scale and inference within an ecosystem.

Plant biodiversity pattern across space may also be an artefact of the ecological association of different specialist plant growth forms to heterogeneous microsite conditions, as generated by ecological processes such as fire or predation (Kirkpatrick *et al*. 1988; Thomson *et al*. 1997). Various levels of fire disturbance can significantly explain variation in vegetation structure and composition of fire-climatic ecosystems such as grasslands (Bond & Keeley 2005). Annual fires within managed South African montane grassland remnants significantly influence plant distribution (O'Connor *et al*. 2009). Differences in fire regime, whether in intensity, severity, frequency or seasonality, can select for specific plant attributes within a burnt ecosystem (Bond & Keeley 2005). Specifically, the demography of some geophyte species within rocky grasslands in France has been described as a function of fire, where their dispersion pattern could be explained through the intermediate disturbance hypothesis (Diadema *et al*. 2007). Similarly, perennial grasses are sensitive to severe defoliation, especially during certain phenological stages, and variable fire disturbance could therefore influence their presence or absence within a community (Sarmiento 1992). Rocky areas have been implicated in lessening the disturbance factor (by reduced fire intensity and severity) and thereby providing refugia for many fire sensitive species (Signell & Abrams 2006). In turn, this could drive the observed differences in geophyte and perennial grass species richness (and overall plant species richness) between low and high percentage rockiness (*sensu* Kirkpatrick *et al*. 1988).

In addition, there is evidence that the higher geophyte species richness in certain rocky areas might also be due in part to predation. In the United States, Thomson *et al*. (1996) showed how a burrowing gopher species was more prevalent in moist deep-soil pockets rather than in rocky outcrops within the same landscape, while its food plant (a geophyte) was more prevalent within the rocky outcrops, indicating the physical constraint on the animal in rocky soils was to the benefit of the plant species. Grassland systems in South Africa do have burrowing golden moles and mole-rats (Skinner & Chimimba 2005), both of which eat bulbs

and could be hindered by rocky soils. Whether predation, in addition to fire, also contributes to rockiness in explaining geophyte distribution within this particular grassland ecosystem remains to be explored.

Conclusion

Maintaining biodiversity is essential for promoting sustainability of an ecosystem (Tilman *et al*. 2006). Furthermore, to understand and conserve biodiversity patterns, we also need to understand the drivers of species dispersion in space and time (Gaston 2000). Here, I provide insight into a phenomenon where a physical abiotic factor, amount of rockiness at the meso-scale, helps explain variable plant biodiversity patterns across the landscape within African montane grasslands. I propose that the higher plant species richness observed in areas of higher percentage rockiness could be explained by rockiness creating higher habitat heterogeneity which leads to localised species specialisation. Moreover, certain plant growth forms' (geophytes and perennial grasses) association with rockiness are the main contributors to this observed difference in spatial dispersion of species richness. Thus, when an abiotic feature such as rockiness is observed across a landscape, it provides a picture of the spatial heterogeneity of certain plant life-form types, and aids in highlighting plant biodiversity hotspots within these grasslands. This meso-scale study also highlights the importance of including rocky landscapes, as a surrogate for plant diversity, when delineating protected areas within this montane grassland ecosystem. Further studies concerning ecological processes such as fire and predation, which seem to be confounding variables for this plant biodiversity-rockiness pattern at a landscape scale (*sensu* Thomson *et al*. 1996), is encouraged.

References

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46

Armstrong, A.J., van Hensbergen, H.J. & Geertsema, H. (1994) Evaluation of afforestable

montane grasslands for wildlife conservation in the north-eastern Cape, South Africa. Part 1. Methods. *South African Forestry Journal*, **171**, 7-20

Auerbach, M. & Shmida, A. (1987) Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution*, **2**, 238-242

Bieringer, G. & Zulka, K.P. (2003) Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae andAcrididae) assemblage of an adjacent dry grassland. *Biodiversity and Conservation*, **12**, 1481-1495

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387-394

Bruun, H.H. (2000) Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography*, **23**, 641-650

Bruun, H.H., Moen, J. & Angerbjörn, A. (2003) Environmental correlates of meso-scale plant species richness in the province of Härjedalen, Sweden. *Biodiversity and Conservation*, **12**, 2025-2041

Cantero, J.J., Liira, J., Cisneros, J.M., Gonzalez, J., Nuñez, C., Petryna, L., Cholaky, C. & Zobel, M. (2003) Species richness, alien species and plant traits in Central Argentine mountain grasslands. *Journal of Vegetation Science*, **14**, 129-136

Diadema, K., Médail, F. & Bretagnolle, F. (2007) Fire as a control agent of demographic structure and plant performance of a rare Mediterranean endemic geophyte. *Comptes Rendus Biologies*, **330**, 691-700

Dorrough, J. & Scroggie, M.P. (2008) Plant responses to agricultural intensification. *Journal of Applied Ecology*, **45**, 1274-1283

Dufour, A., Gadallah, F., Wagner, H.H., Guisan, A. & Buttler, A. (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography*, **29**, 573-584

English, N.B., Weltzin, J.F., Fravolini, A., Thomas, L. & Williams, D.G. (2005) The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments*, **63**, 324-343

Everson, C.S. & Clarke, G.P.Y. (1987) A comparison of six methods of botanical analysis in the montane grasslands of Natal. *Vegetatio*, **73**, 47-51

Frank, D.A. & McNaughton, S.J. (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos*, **62**, 360-362

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227

Gee GW, Bauder JW (1986) Particle size analysis. In: Klute A (ed) *Methods of soil analysis*, No. 9, Part 1, American Society of Agronomy, Madison, Wisconsin, USA

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009

Hadar, L., Noy-Meir, I. & Perevolotsky, A. (1999) The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. *Journal of Vegetation Science*, **10**, 673-682

Hayes, G.F. & Holl, K.D. (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology*, **17**, 1694-1702

Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D., Gaedke, U., Legendre, P., Magnuson, J.J., McArdle, B.H., Muldavin, E.H., Noble, D., Russell, R., Stevens, RD., Willis, T.J., Woiwod, I.P. & Wondzell, S.M. (2007) Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Science USA*, **104**, 3273-3277

Kirkpatrick, J.B., Fensham, R.J., Nunez, M. & Bowman, D.M.J.S. (1988) Vegetation-radiation relationships in the wet-dry tropics: granite hills in northern Australia. *Vegetatio*, **76**, 103-112

Kuo S (1996) Phosphorus. In: Sparks DL (ed) *Methods of Soil Analysis, Part 3, Chemical Methods*, Soil Science Society of America, Madison, Wisconsin, USA

Lambrinos, J.G., Kleier, C.C. & Rundel, P.W. (2006) Plant community variation across a puna landscape in the Chilean Andes. *Revista Chilena de Historia Natural*, **79**, 233-343

Landi, M., Frignani, F., Lazzeri, C. & Angiolini, C. (2009) Abundance of orchids on calcareous grasslands in relation to community species, environmental, and vegetational conditions. *Russian Journal of Ecology*, **40**, 486-494

Maccherini, S. (2006) Factors associated with species richness in a remnant calcareous grassland. *Grassland Science*, **52**, 181-184

McCulloch, C.E., Searle, S.R. & Neuhaus, J.M. (2008) *Generalized, linear, and mixed models*. Wiley, USA

McNatty, A., Abbott, K.L. & Lester, P.J. (2009) Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands. *Oecologia*, **160**, 187-194

Montaña, C. (1990) A floristic-structural gradient related to land forms in the southern

Chihuahuan desert. *Journal of Vegetation Science*, **1**, 669-674

Mucina, L. & Rutherford, M.C. (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria

O'Connor, T.G., Uys, R.G., Mills, A.J. (2004) Ecological effects of fire-breaks in the montane grasslands of the southern Drakensberg, South Africa. *African Journal of Range and Forage Science*, **21**, 1-9

Palmer, M.W. (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica and Phytotaxonomica*, **29**, 511-530

PRIMER-E (2008) *PERMANOVA and PRIMER 6*. PRIMER-E, Lutton

Pryke, J.S. & Samways, M.J. (2012) Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology*, **27**, 73-85

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, 405, 212-219

Rich, T., Rebane, M., Fasham, M., McGeechan, F. & Dobson, D. (2005) Methods for surveying habitats: ground and shrub vegetation. In: Hill D, Fasham M, Tucker G, Shewry M, Shaw P (eds) *Handbook of Biodiversity Methods: survey, evaluation and monitoring*, Cambridge University Press, Cambridge, UK

Roxburgh, S.H., Shea, K. & Wilson, J.B. (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*, **85**, 359-371

Sarmiento, G. (1992) Adaptive strategies of perennial grasses in South American savannas. *Journal of Vegetation Science*, **3**, 325-336

Shapiro, S.S. & Wilk, M.B. (1965) An analysis of variance test for normality (complete samples). *Biometrika*, **52**, 591-611

Signell, S.A. & Abrams, M.D. (2006). Influence of rocky landscape features and fire regime on vegetation dynamics in Appalachian *Quercus* forests. *Journal of Vegetation Science*, **17**, 675-684

Skinner, J.D. & Chimimba, C.T. (2005) *The Mammals of the Southern African Subregion*, Cambridge University Press, Cambridge

Stohlgren, T.J. & Bachand, R.R. (1997) Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology*, **78**, 632-641

Thomson, J.D., Weiblin, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698-1715

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a

decade-long grassland experiment. *Nature*, **441**, 629-632

Tucker, G., Fasham, M., Hill, D., Shewry, M., Shaw, P. & Wade, M. (2005) Planning a programme. In: Hill D, Fasham M, Tucker G, Shewry M, Shaw P (eds) *Handbook of Biodiversity Methods: survey, evaluation and monitoring*, Cambridge University Press, Cambridge, UK

Turner, M.G. & Dale, V.H. (1998) Comparing large, infrequent disturbances: what have we learned? *Ecosystems*, **1**, 493-496

Whalley, R.D.B. & Hardy, M.B. (2000) Measuring Botanical Composition of Grasslands. In: 't Mannetje L, Jones RM (eds) *Field and Laboratory Methods for Grassland and Animal Production Research*, CABI Publishing, UK

Chapter 4

Grasshopper assemblage response to the rocky mesofilter in Afro-montane grasslands

Abstract

The distribution of physical features in a landscape often explains local species dispersion patterns, and these features could be important for conservation planning. Grasshoppers are often an important functional component of an ecosystem, and many species show high levels of endemism. Evidence exists that rockiness within a landscape can predict diversity of grasshopper species. However, why grasshopper species should respond to rocky landscapes has not been established. Here, I explore whether grasshoppers are responding to physical rockiness per se, or rather to specific correlates of higher rock exposure within a landscape. I also determine if this response varies between grasshopper taxonomic groups. I sampled grasshoppers in the semi-natural montane grasslands in KwaZulu-Natal, South Africa, and recorded ten environmental variables. I explored the influence of these variables on grasshopper community composition and grasshopper family composition. I also determined the significant vegetation correlates of higher rockiness in this landscape, and then measured the similarity of species composition across these correlates. Overall, grasshopper assemblage composition, as well as familial composition, responded to the significant vegetation correlates of rockiness (vegetation density, geophyte species richness and perennial grass species richness) rather than to the rockiness per se. This finding was consistent across the most abundant families or subfamilies. Across taxonomic groups, there are specialist species within each group which are associated with environmental conditions related to rockiness and its underlying correlates. Rock exposure across this grassland landscape is therefore an important contributor to grasshopper dispersion patterns, and has important implications for conservation planning for this taxon.

Introduction

Exploring the determinants of biodiversity patterns across multiple scales is a central tenet in conservation ecology (Gaston 2000). Furthermore, the delineation of protected areas requires an in-depth understanding of species dispersions across space and time (Rodrigues *et al*. 2004). This means that for conservation to take place, we need to identify the main drivers of the diversity and distribution of species (Richardson 2012). However, studying dispersion patterns for all taxa within an ecosystem is often impossible, mainly due to the ongoing rapid change in the natural environment and the consequent loss of ecosystems and species (Sala *et al*. 2000). Consequently, optimized decision-making tools are required which relate to protected area design and management (Sarkar *et al*. 2006). In turn, this has stimulated use of surrogates of biodiversity, so as to more readily predict which areas are of conservation concern as opposed to timeous whole inventories across multiple landscapes (Rodrigues & Brooks 2007).

Biodiversity surrogates can either be of biotic or abiotic nature, although cross-taxon surrogacy has been shown to be stronger than surrogates based on environmental data (Rodrigues & Brooks 2007). Nonetheless, environmental surrogates are useful for biodiversity conservation planning, as they can successfully predict areas of conservation concern at multiple spatial scales (Sarkar *et al*. 2005). Indeed, various environmental factors, measured at the meso-scale, have been shown to be greatly influential on species distribution patterns across landscapes (Samways 1990; Heikkinen 1996; Bruun *et al*. 2003). Essentially, certain ecosystem features have great potential in delineating or prioritizing areas of conservation concern across various ecosystems (Wessels *et al*. 1999; Oliver *et al*. 2004; Hewitt *et al*. 2005; Barton *et al*. 2009). As such, environmental variables could therefore be considered important mesofilters, and subsequently be valued in the design and management of protected areas (Hunter 2005).

Grasshoppers (Orthoptera) are important organisms affecting ecological processes within grassland landscapes, and therefore necessitate appropriate conservation (Samways 1997), especially as these landscapes are often variegated. Variegated landscacpes suggest that eurytopic or cosmopolitan species are likely to perceive the landscape as a continuum of ecosystem elements of varying suitability towards their life-cycle needs, whereas stenotopic species would have a narrower tolerance to varying habitat conditions (McIntyre & Barrett 1992; Ingham & Samways 1996). Therefore, biodiversity management within semi-natural

environments requires identification and understanding of the key ecosystem elements (mesofilters) that determine different grasshopper dispersal responses in space. This means identifying the necessary variety of biotopes so as to fully conserve overall grasshopper diversity (Samways 1997; Wettstein & Schmid 1999; Samways & Kreuzinger 2001).

Grasshopper assemblages respond to multiple environmental conditions within a landscape, and are often highly sensitive to changes in these conditions (Samways & Sergeev 1997). Environmental conditions that influence grasshopper assemblages include regional climatic variation (Telfer & Hassal 1999), topographical traits such as elevation or aspect as proxies for microclimatic events (Samways 1990; see also Hodkinson 2005), plant architectural traits such as vegetation height and plant community structural traits such as vegetation density (Joern 1982; van Wingerden *et al*. 1991), and even plant nutrient availability (Loaiza *et al*. 2011). Furthermore, ecological processes, such as fire and grazing, are known to influence grasshopper community responses, as these disturbances, at variable levels, not only induce plant compositional change, but also create heterogeneity in plant structural attributes (Chambers & Samways 1998; Samways & Kreuzinger 2001; Joern 2004, 2005). Essentially, microhabitat heterogeneity is an important determinant of grasshopper spatial dynamics (Guido & Gianelle 2001), especially when microhabitat heterogeneity is correlated with microclimatic heterogeneity (Willott 1997).

A physical ecosystem feature, rockiness, was shown to influence grasshopper communities in montane grasslands (Chapter 2), and in a grassland-karoo ecotone in South Africa (Gebeyehu & Samways 2002). This suggests that if we conserve rocky areas in a landscape, we can also conserve certain orthopteran populations (a rocky mesofilter). However, the question of why rockiness influences grasshopper dispersion patterns has not been resolved. This leads to the question of whether it is the rockiness *per se* influencing grasshopper assemblage in some instances, or rather specific correlates of higher rock exposure. Here, I explore the possible reasons why rockiness influences the local distribution of grasshopper species. In addition, I ask how the various species respond relative to their taxonomic groups. Through asking these questions, we gain an understanding of the functional aspects of grasshopper dispersion across a landscape. I further investigate the concept of a rocky mesofilter, to explore whether there are other associated underlying filters driving this grasshopper-rockiness observation within this montane grassland. These results would then have application in biodiversity planning and management of this and other taxa.

Methods

Study area

The study was conducted within the 16 000 ha Merensky Forestry estate at Weza, near Kokstad, KwaZulu-Natal, South Africa. Around 4 200 ha are semi-natural open spaces, the remainder being commercial forestry. The open spaces lie mostly within the endangered Midlands Mistbelt Grassland vegetation type (Mucina & Rutherford 2006). The endangered status of this vegetation type is mainly driven by large forestry plantations in the area. The dominant grass in the area is *Themeda triandra* Forssk. All selected sites are classified as semi-natural, as all were annually burned by forestry management over >6 decades. This frequency produces a dense productive grassland (Tainton & Mentis 1984), which equates to the natural burning regime in the area of between one and ten ground lightning flashes km^{-2}yr^{-1} (Edwards 1984). The geology is sand and siltstones from the Ecca group. Weathered resistant dolerite dykes are also present. The maximum height of the mountains is 2 200 m a.s.l., above an undulating landscape with minimum elevation of 900 m a.s.l.

This is a summer rainfall region, where most precipitation occurs between November and March. Annual precipitation varies around 1000 mm per annum in the low lying areas, to 1500 mm on the mountain peaks. Mean daily maximum temperature ranges from 17.6˚C in June to 26˚C in January. Mean daily minimum temperatures range from 0.1˚C in June to 13.4˚C in January.

Grasshopper sampling

Grasshoppers were sampled from 18 sites (see Fig. 2.1, Chapter 2) within the semi-natural areas across the sampling area. All sampling was done >30 m away from the plantation forest edge to reduce sampling bias due to edge effects (Samways & Moore 1991; Bieringer & Zulka 2003; Pryke & Samways 2012). Sampling was twice, January and April 2011, to cover the major seasons for grasshoppers. Grasshoppers were sampled by sweep netting, which for short, dense vegetation types such as grasslands, are adequate (Gardiner *et al*. 2005). Two 100 m transects were laid out. Parallel to each side of each transect, one hundred 180˚ sweeps were made with a mesh net (diameter 40 cm). This rendered 200 sweeps per transect, and ultimately 800 sweeps per site over the study period. To ensure adequate taxon representation,

sampling was conducted until the species accumulation curve near flattened (Gotelli & Colwell 2001) (Appendix B). Grasshoppers were identified to family, subfamily and species (or morphosepcies) level according to Dirsh (1965) and Eades *et al*. (2011).

Environmental variables

Environmental variables included in this study were elevation, aspect (north, south and neutral, where neutral constitutes a ridge or a valley), vegetation height, vegetation density, distance to a river, perennial grass richness, geophyte richness, and percentage rocks.

To obtain values for vegetation height, vegetation density, perennial grass richness, geophyte richness and percentage rocks, I used point intercept line transects, as this method is relevant and insightful for biodiversity studies in these grasslands (Everson & Clarke 1987; Armstrong *et al*. 1994). Field methods were similar to Hayes & Holl (2003), where a measuring tape, 50 m long, was used to record all plant species which intercept a 1.8 mm-diameter pin every 1 m (51 points per transect). In addition, a one meter belt, perpendicular to the line transect, was time-searched (15 min) after each transect measurement, as a means for recording a more comprehensive species list that could include short lived annual plants (Hayes & Holl 2003). A total of four 50 m transects were placed within each of the eighteen sites, each transect being 15 m away from another, effectively having 204 points per site.

Geophyte richness and perennial grass richness per site was estimated through categorizing the recorded species as either geophytes or perennial grasses as these two growth forms have a particular association with the rocky mesofilter (Chapter 3). Percentage rockiness was measured as followed: when rocks were touched by the pin in transects, they were added and then divided by the total number of hits (204) and percentage rockiness was then calculated. Vegetation height was recorded every five meters within transects, rendering 40 height measurements per site. To obtain these values, a lightweight plastic disc with a hole in the center was dropped over the pin onto the vegetation, and height subsequently measured on the pin. Vegetation density was measured through dividing the number of plant individuals that touched the pin per site by the total number of pin hits per site (as per Joern 1982).

Elevation and aspect were measured on site with a handheld GPS (GPS 72, Garmin International, Inc.). Distance to river was calculated through surveying images of the study area in Google Earth (Google, Inc.), and measured as the distance in meters from the center of each site to the nearest river.

Statistical analysis

To examine the possible relationships between percentage rock exposure and vegetation variables, a non-parametric Spearman rank correlation matrix reporting r-values was constructed (Statistica Release 10, StatSoft, Inc.). In turn, to determine the influence of the environmental variables on species assemblage composition, a canonical correspondence analysis (CCA) was performed using CANOCO 4.5 (ter Braak & Šmilauer 2002). A further CCA was then performed to examine the influence of the same environmental variables on the different grasshopper taxonomic groups. For this CCA, only families or subfamilies having more than two individuals were included. Then, a rank abundance of grasshopper family (or subfamily within Acrididae) was constructed to obtain the six most abundant groups (Fig. 4.1). A separate CCA was then performed for each of the six most abundant groups. However, Tettigoniidae, which ranks high in abundance, was not used as its dominance was due to one species. Forward selection during the CCA analysis was then used to rank the four most important environmental variables that structure species distribution within each of the six most abundant families or subfamilies. However, within two groups, Catantopinae and Tetrigidae, less variables were selected as these groups had fewer species than environmental variables.

Furthermore, to explore whether differences in grasshopper species composition exist across significant vegetation correlates of rock exposure within the landscape, I used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) in PRIMER 6 (PRIMER-E 2008). PERMANOVA results are reported as F- and *P*-values (e.g. McNatty *et al*. 2009), where a significant *P*-value indicates a significant difference (at the 5% level) between levels (groups) of a studied factor. In addition, I also performed a canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003) for each of the vegetation correlates of rockiness in PRIMER 6 (PRIMER-E 2008). CAP allows visualization of patterns of community differences across certain treatments, and also whether the observed spread of a group is by chance alone through cross validation by 'leave-one-out' allocations (e.g. Messmer *et al*. 2011). For these statistics, I categorized percentage rockiness as higher or lower than 10% rocky (>10 or <10); vegetation density as 128-154% as low density (LD) and 160-208% as high density (HD); perennial grass richness as 8-12 species as low perennial grass (LPG) and 14-19 species as high perennial grass (HPG); and geophyte richness as 4-9 species as low geophytes (LG) and 11-17 species as high geophytes (HG). All these

categories were chosen as they represent higher or lower than the mean within each dataset. Both PERMANOVA and CAP analyses were performed using Bray-Curtis similarity measures where data for each group were fourth-root transformed to reduce the weight of the common species (Anderson 2001).

Results

A total of 48 species was observed across all 18 study sites (Table 4.1). Within the Acrididae, the Acridinae was by far the most abundant group (Fig. 4.1), mainly driven by the high abundance of two species, *Orthochtha* sp. 1 and *Coryphosima stenoptera* (Schaum) (Table 4.1).

Table 4.1 Recorded adult species, their abbreviations used in CANOCO analysis, as well as prevalence and abundance (14400 sweep-net samples) across 18 Afro-montane grassland sites

Species	Abbreviation	No. sites occupied	Abundance
Acanthoxia natalensis (Krauss)	Acna	1	2
Acorypha ferrifer (Walker)	Acfe	5	9
Acrida sp.1	Acs1	4	8
Anthermus granosus (Stål)	Angr	6	14
Austrodontura capensis (Walker)	Auca	1	4
Calliptamicus semiroseus (Serville)	Case	5	6
Catantops melanostictus (Schaum)	Came	1	1
Conocephalus caudalis (Walker)	Coca	12	43
Coryphosima stenoptera (Schaum)	Cost	14	66
Dictyophorus spumans (Thunberg)	Disp	1	2
Dirshia abbreviata (Brown)	Diab	5	18
Dnopherula callosa (Karsch)	Dnca	14	42
Eremidium equuleus (Karsch)	Ereq	3	6
Eucoptacra turneri (Miller)	Eutu	5	8
Euryphiminae sp. 1	Eus1	2	2
Eyprepocnemis calceata (Serville)	Eyca	3	3
Faureia milanjica (Karsch)	Fami	6	24
Gastrimargus determinatus vitripennis (Saussure)	Gadv	1	1
Gastrimargus drakensbergensis (Ritchie)	Gadr	7	10
Gastrimargus wahlbergii (Stål)	Gawa	4	5

Gymnobothrus linea-alba (Bolívar)	Gyli	3	5
Gymnobothrus temporalis (Stål)	Gyte	5	15
Heteracris sp. 1	Hes1	6	9
Heteropternis guttifera (Kirby)	Hegu	7	12
Humbe tenuicornis (Schaum)	Hute	1	2
Lentula callani (Dirsh)	Leca	2	4
Lentula minuta (Dirsh)	Lemi	7	17
Lentula obtusifrons (Stål)	Leob	1	1
Machaeridia conspersa (Bolívar)	Maco	9	24
Maura rubroornata (Stål)	Maru	1	1
Weenenia lineata (Brown)	Weli	1	6
Ornithacris cyanea (Stoll)	Orcy	1	1
Orthochtha sp. 1	Ors1	17	107
Orthochtha sp. 2	Ors2	2	4
Parga xanthoptera (Stål)	Paxa	2	2
Phaeocatantops sulphurous (Walker)	Phsu	2	2
Pnorisa squalus (Stål)	Pnsq	5	10
Pseudoarcyptera cephalica (Bolívar)	Psce	1	3
Qachasia fastigata (Dirsh)	Qafa	4	5
Saginae sp. 1	Sas1	1	1
Scintharista rosacea (Kirby)	Scro	1	1
Tetrigidae sp. 1	Tes1	2	6
Tetrigidae sp. 2	Tes2	3	17
Tetrigidae sp. 3	Tes3	11	101
Thericleidae sp. 1	Ths1	6	10
Thyridota sp. 1	Tys1	1	2
Vitticatantops botswana (Jago)	Vibo	12	51
Zuludectus modestes (Péringuey)	Zumo	1	2

Table 4.2 Spearman rank correlation matrix of r-values comparing the relationships among measured vegetation traits and percentage rockiness.

	Vegetation Density	% Rock	Vegetation Height	Geophyte Richness	Perennial Grass Richness
Vegetation Density	1.000000	**-0.532783**	-0.073271	**-0.496115**	**-0.469160**
% Rock		1.000000	0.156944	**0.823123**	**0.674766**
Vegetation Height			1.000000	0.304741	-0.120432
Geophyte Richness				1.000000	**0.607930**
Perennial Grass Richness					1.000000

Values in bold are significant at the 5% level
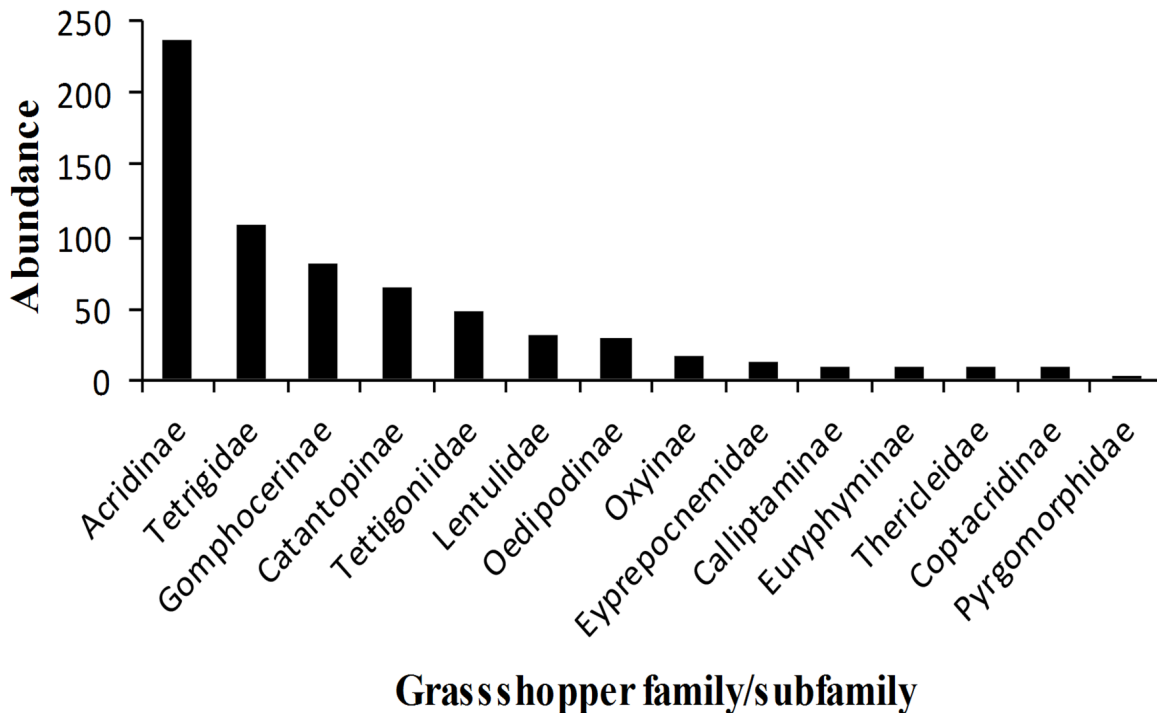
Figure 4.1 Rank abundance of each recorded grasshopper family (or subfamilies within the Acrididae) across the 18 studied semi-natural montane grassland sites

It was clear that percentage rockiness alone did not influence the species distribution, but rather that the significant vegetation correlates of rockiness such as vegetation density, geophyte richness and perennial grass richness (as per Table 4.2) did (Fig. 4.2). Furthermore, elevation and vegetation height also had a marked influence on the distribution of grasshopper species across the landscape (Fig. 4.2). The different grasshopper taxonomic groups followed a similar trend in response to the environmental variables that resulted in the species patterns in the CCA (Fig. 4.3). Particularly, elevation and the significant vegetation correlates of rockiness were the most important variables shaping the local distribution patterns of the six most abundant grasshopper families (or subfamilies within the Acrididae), with the exception of the Tetrigidae (Fig. 4.4a-f). More specifically, elevation and vegetation density were the two most important variables, with the Acridinae, Gomphocerinae and Lentulidae all being greatly influenced by both these variables. In addition, vegetation density was the most important variable driving the Oedipodinae. Percentage rockiness *per se* and vegetation density together was consistently influential on the local distribution of both the Acrididae and Lentulidae (Fig. 4.4a, b).
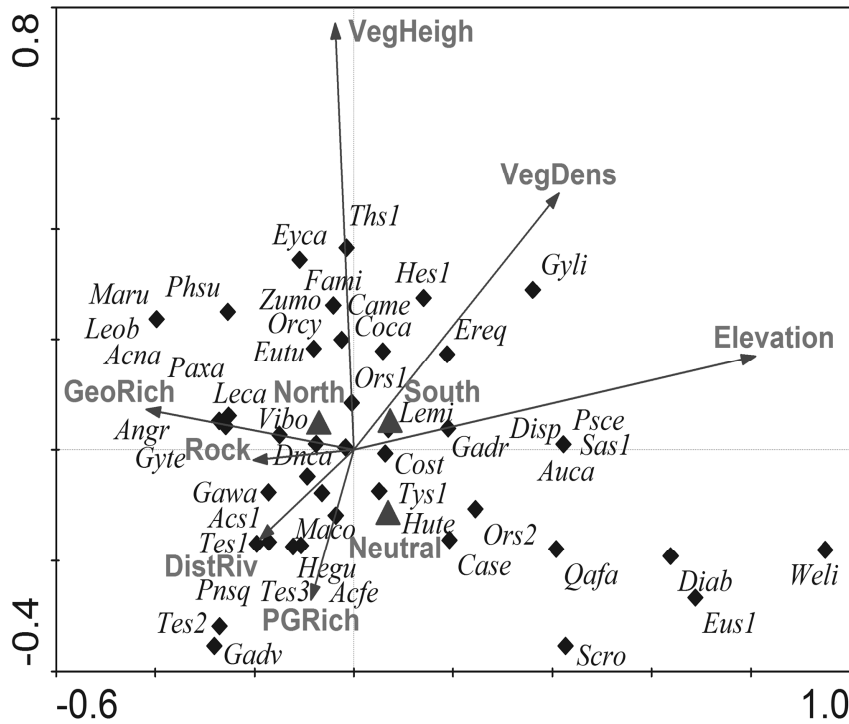
Figure 4.2 Canonical correspondence analysis (CCA) ordination for all recorded grasshopper species and measured environmental variables. Aspect is labeled as North, South or Neutral when it constitutes a ridge or a valley. Rock, percentage rock exposure within a site; VegHeigh, vegetation height; VegDens, vegetation density; PGRich, perennial grass richness; GeoRich, geophyte richness; DistRiv, distance to river. Species abbreviations as in Table 4.1.
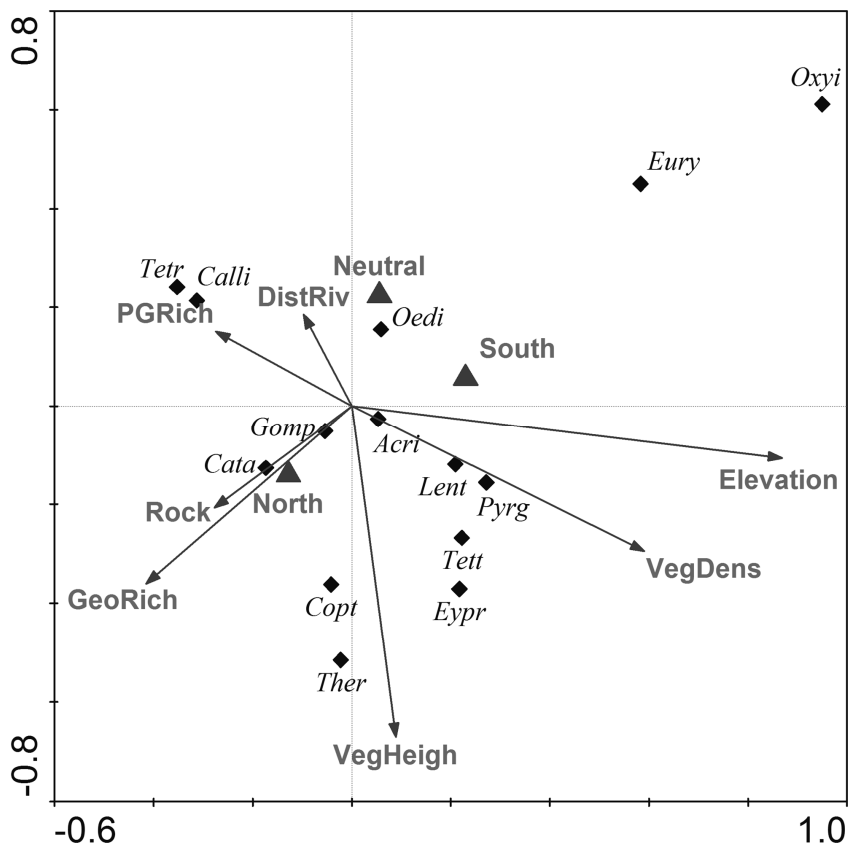
Figure 4.3 Canonical correspondence analysis (CCA) ordination for grasshopper families (or subfamilies within the Acrididae) and measured environmental variables. Aspect is labeled as North, South or Neutral. Neutral constitutes a ridge or a valley. Rock, percentage rock exposure within a site; VegHeigh, vegetation height; VegDens, vegetation density; PGRich, perennial grass richness; GeoRich, geophyte richness; DistRiv, distance to river. Acri, Acridinae; Calli, Calliptaminae; Cata, Catantopinae; Copt, Coptacridinae; Eury, Euryphyminae; Eypr, Eyprepocnemidae; Gomp, Gomphocerinae; Lent, Lentulidae; Oedi, Oedipodinae; Oxyi, Oxyinae; Pyrg, Pyrgomorphidae; Tett, Tettigoniidae; Tetr, Tetrigidae; Ther, Thericleidae
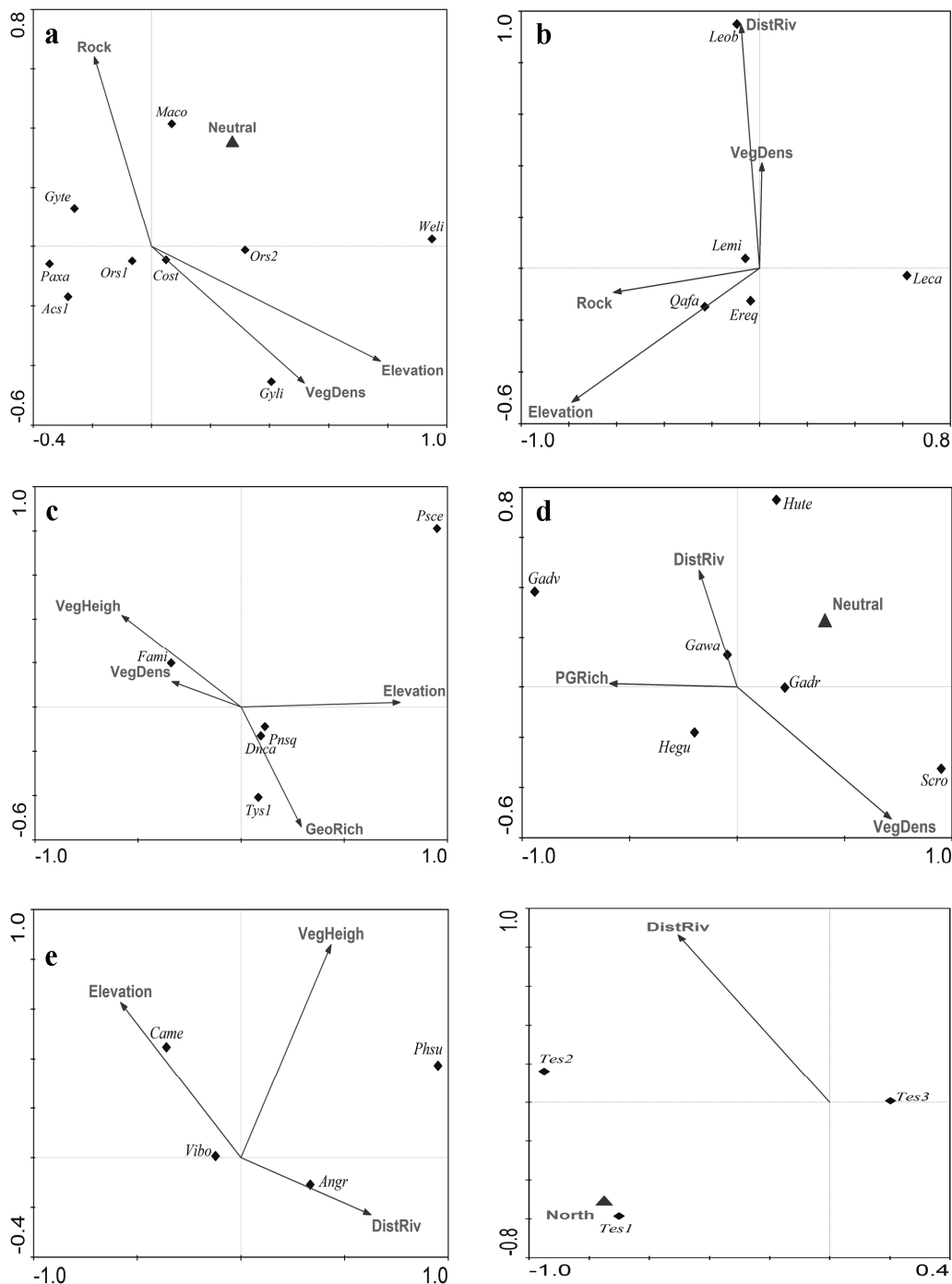
Figure 4.4 Canonical correspondence ordination (CCA) for the six most diverse and abundant grasshopper families (or subfamilies within the Acrididae) and the environmental variables most affecting their distribution. a) Acridinae; b) Lentulidae; c) Gomphocerinae; d) Oedipodinae; e) Catantopinae; and f) Tetrigidae. Aspect is North, South or Neutral. Neutral is a ridge or a valley. Rock, percentage rock exposure within a site; VegHeigh, vegetation height; VegDens, vegetation density; PGRich, perennial grass richness; GeoRich, geophyte richness; DistRiv, distance to river. Species abbreviations as in Table 4.1.

Table 4.3 PERMANOVA analyses of the influence of a vegetation density, geophyte richness and perennial grass richness factor on grasshopper species composition across all sites

Factor	*P*-value
Vegetation Density	0.3292
Geophyte Richness	0.0764
Perennial Grass Richness	0.7653

Table 4.4 Cross validation that the observed spread of groups, as per Fig. 4.5, is not by chance alone through 'leave-one-out' allocation in the CAP analysis

Group	% Correct	Misclassification Error (%)
*Vegetation Density*Rockiness*		
HD>10	0	100
LD<10	0	100
LD>10	83.333	16.667
HD<10	62.5	37.5
*Geophyte Richness*Rockiness*		
HG>10	75	25
LG<10	44.444	55.556
HG<10	100	0
*Perennial Grass Richness*Rockiness*		
HPG>10	57.143	42.857
LPG<10	25	75
HPG<10	33.333	66.667
LPG>10	0	100

>10 or <10, higher or lower than ten percent rockiness; LD or HD; vegetation density low (128-154%) or high (160-208%); LPG or HPG, perennial grass richness as low (8-12 species) or high (14-19 species), LPG or HPG, geophyte richness as low (4-9 species) or high (11-17 species)

Overall, there was no significant difference in grasshopper species composition across all sites when tested against the significant vegetation correlates of rockiness ($P > 0.05$) (Table 4.3). In turn, CAP analysis showed that when rockiness was combined with its significant vegetation correlates, clear assemblage groupings were observed across each tested factor (Fig. 4.5a-c). Moreover, consistent with the PERMANOVA result, none of the treatments (Fig 4.5a-c) showed significant assemblage differences ($P = 0.118$, $P = 0.267$ and $P = 0.053$ respectively). More specifically, the spread of the groupings of >10% rockiness and

low vegetation density and >10% rockiness and high geophyte richness are not likely to be by chance alone, as both factors had a low misclassification error (Table 4.4).
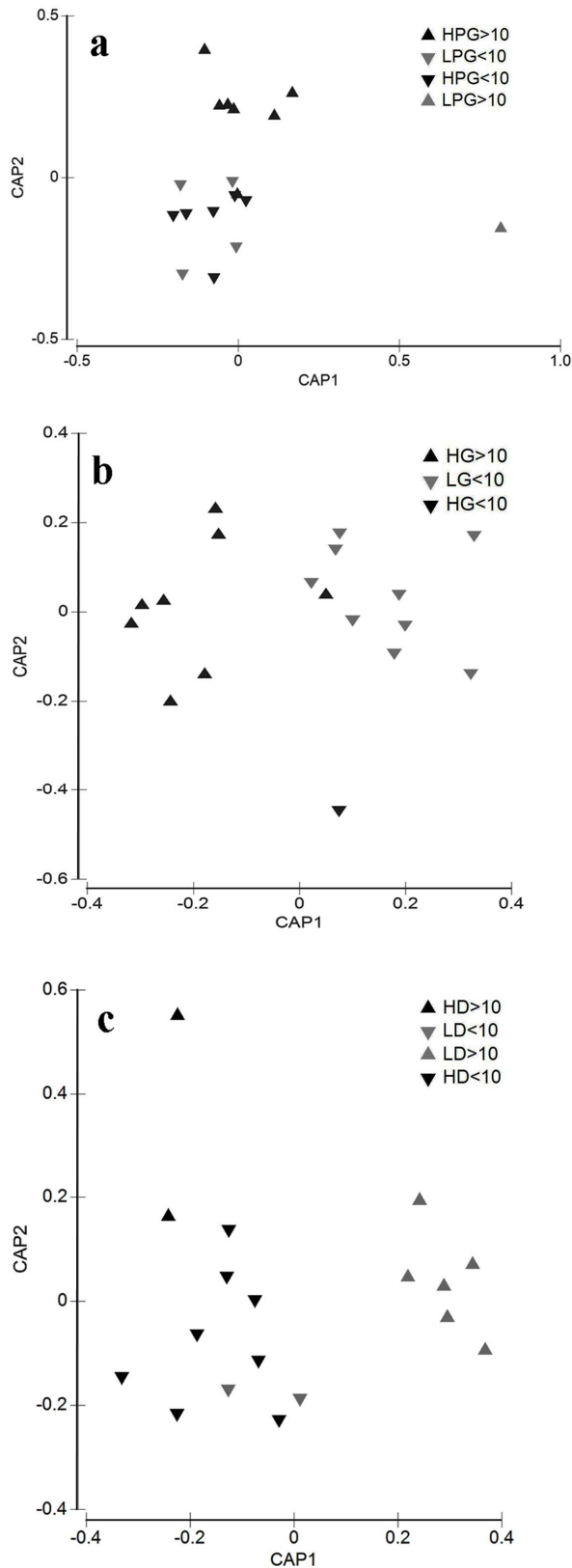
Figure 4.5 Canonical analysis of principal coordinates (CAP) ordination plots of grasshopper assemblage data across the rockiness correlates of a) perennial grass richness, b) geophyte richness and c) vegetation density. >10 or <10, higher or lower than ten percent rockiness; LD or HD; vegetation density low (128-154%) or high (160-208%); LPG or HPG, perennial grass richness as low (8-12 species) or high (14-19 species); LPG or HPG, geophyte richness as low (4-9 species) or high (11-17 species)

Discussion

Grasshoppers are particularly responsive to a variety of environmental conditions, which is why microhabitat heterogeneity is an important determinant of grasshopper spatial patterns (Samways & Sergeev 1997; Guido & Gianelle 2001). Here, I show why grasshoppers respond to a rocky mesofilter, directly and indirectly, which in turn, helps explain the dispersion patterns of this taxon across a semi-natural montane grassland landscape.

Percentage rock exposure is known to strongly influence grasshopper dispersion patterns in South Africa (Chapter 2; Gebeyehu & Samways 2002). However, here the canonical correspondence analyses for both species and families (or subfamilies within the Acrididae), showed that although some species did respond to increased rockiness, it was not so much rockiness *per se* driving grasshopper dispersion patterns across this landscape, but rather the underlying vegetation correlates of having higher rock exposure within a patch. Specifically, this was attributed to vegetation density, which influenced and predicted the presence/absence of both certain grasshopper species individually, and certain grasshopper taxonomic groups across the landscape. Furthermore, CAP analysis confirmed that the combination of higher rockiness and low vegetation density delineated a specific group of species associated with these environmental conditions. This finding was also strong for high rockiness and high geophyte richness. Essentially, grasshoppers respond to the rocky mesofilter through partially responding to the rockiness itself, but mostly indirectly, by responding to the vegetation structural correlates of high rock exposure within an ecosystem.

In addition, vegetation height, albeit not a significant correlate of rockiness, was also an important variable. However, the effect of variable vegetation density and height on grasshopper dispersion patterns is well reported in literature (Joern 1982; van Wingerden *et al*. 1991, 1992; Wettstein & Schmid 1999). Furthermore, variation in vegetation structure is strongly linked to temperature heterogeneity, where too little light exposure negatively affects some grasshopper species relating to egg and nymph development (van Wingerden *et al*. 1991, 1992). In turn, such species avoid such low light conditions, and hence certain areas within a landscape. Indeed, a relationship between thermoregulatory ability and habitat partitioning is a known phenomenon in grasshoppers (Willot 1997). In South African montane grasslands, Samways (1990) showed the influence of temperature, as a function of varying topography, on the local distribution of grasshoppers across the landscape. Essentially, higher levels of rockiness indicate higher habitat heterogeneity, and consequently

more variable microsite conditions which suggests more complex resource differentiation and species specialization (as per Auerbach & Shmida 1987).

The use of an abiotic surrogate, such as a rocky mesofilter, has received some critique. Biotic surrogates are often seen as performing better than environmental surrogates (Rodrigues & Brooks 2007). However, here I show that environmental variables such as rockiness and its vegetation correlates of density, geophyte richness, and perennial grass richness, are influential on the distribution of the most abundant families (or subfamilies within Acrididae). Specifically, the rocky mesofilter ranked high in structuring the assemblages of Acridinae (which was the most diverse and abundant group), Gomphocerinae, Lentulidae and Oedipodinae. Thus, the rocky mesofilter was important in predicting the presence/absence of species across multiple taxonomic groups. This environmental surrogate could therefore be seen as an important consideration in grasshopper biodiversity conservation (*sensu* Sarkar *et al*. 2005).

However, apart from the rocky mesofilter, and its underlying correlates, it was clear that elevation is also an important factor explaining grasshopper assemblage compositional changes across this montane landscape. Furthermore, elevation and the rockiness correlates, when combined, explained most of the spread of the most abundant families. Elevation is seen as a proxy for microclimatic heterogeneity, and is a well-known determinant of grasshopper dispersion patterns in space (Samways 1990; Kemp *et al*. 1990; Wettstein & Schmid 1999; Gebeyehu & Samways 2006). Thus, grasshopper assemblages can respond to multiple environmental conditions within a landscape (Samways & Sergeev 1997). It seems reasonable then, that because so many environmental variables help explain grasshopper dispersion patterns, multiple mesofilters could be delineated for this taxon which would contribute to grasshopper conservation. In particular, elevation also qualifies as a mesofilter in these montane grasslands (although an extension of the classic definition of a mesofilter), which is consistent with elevation explaining arthropod compositional changes across a mountain landscape (Pryke & Samways 2010).

Conclusion

The determinants of biodiversity patterns in space remain a top priority in conservation planning (Gaston 2000). Afro-montane grasshoppers in particular have high levels of

endemism, which emphasizes their conservation priority (Foord *et al.* 2002). Here, I explored why variable levels of rock exposure within a landscape (the rocky mesofilter) influences the local distribution of grasshopper species. Fundamentally, grasshoppers might not be strongly responding to higher rock exposure *per se*, but more towards the heterogeneous conditions created by rockiness within an ecosystem: specifically, the plant community structure (vegetation density) and the higher species richness of certain growth forms which are associated with higher rockiness, such as geophytes and perennial grasses. The grasshopper dispersion patterns observed in this Afro-montane grassland landscape is thus a function of specialist species which are strongly associated with specific microsite conditions, which in this case, are related to the correlates of the rocky mesofilter. In addition, the response of grasshoppers to the rocky mesofilter was also consistent across multiple taxonomic groups, and indicates the use of such a mesofilter as an effective surrogate for grasshopper biodiversity as it represents the majority of species. Moreover, elevation was also as important as the rocky mesofilter in explaining grasshopper dispersion patterns across this montane landscape. Rockiness and elevation are therefore seen as two important environmental parameters pertaining to biodiversity planning and management of grasshoppers for the studied semi-natural Afro-montane grasslands. As such, using mesofilters, as surrogates, could be important in the design and management of protected areas or conservancies (Hunter 2005).

References

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance, *Austral Ecology*, **26**, 32–46.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology, *Ecology*, **84**, 511-525.

Armstrong, A.J., van Hensbergen, H.J. & Geertsema, H. (1994) Evaluation of afforestable montane grasslands for wildlife conservation in the north-eastern Cape, South Africa. Part 1. Methods, *South African Forestry Journal*, **171**, 7-20.

Auerbach, M. & Shmida, A. (1987) Spatial scale and the determinants of plant species richness, *Trends in Ecology and Evolution*, **2**, 238-242.

Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B. & Cunningham, S.A. (2009)

Conserving ground-dwelling beetles in an endangered woodland community: multi-scale habitat effects on assemblage diversity, *Biological Conservation*, **142**, 1701-1709.

Bieringer, G. & Zulka, K.P. (2003) Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland, *Biodiversity and Conservation*, **12**, 1481-1495.

Bruun, H.H., Moen, J. & Angerbjörn, A. (2003) Environmental correlates of meso-scale plant species richness in the province of Härjedalen, Sweden, *Biodiversity and Conservation*, **12**, 2025-2041.

Chambers B.Q. & Samways, M.J. (1998) Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management, *Biodiversity and Conservation*, **7**, 985-1012.

Dirsh, V.M. (1965) *The African genera of Acridoidea*. Cambridge University Press, Cambridge, UK.

Eades, D.C., Otte, D., Cigliano, M.M. & Braun, H. (2011) Orthoptera Species File Online, Version 2.0/4.1. available at http://orthoptera.speciesfile.org.

Edwards, D. (1984) Fire regimes in the biomes of South Africa. *Ecological effects of fire in South African Ecosystems* (ed. by P. de V Booysen and N.M. Tainton), pp 19-37. Springer-Verlag, Berlin.

Everson, C.S. & Clarke, G.P.Y. (1987) A comparison of six methods of botanical analysis in the montane grasslands of Natal, *Vegetatio*, **73**, 47-51.

Foord, S.H., Ferguson, J.W.H. & Van Jaarsveld, A.S. (2002) Endemicity of Afromontane grasshopper assemblages: implications for grassland conservation, *African Journal of Ecology*, **40**, 318-327.

Gardiner, T., Hill, J. & Chesmore, D. (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems, *Journal of Insect Conservation*, **9**, 151-173.

Gaston, K.J. (2000) Global patterns in biodiversity, *Nature*, **405**, 220-227.

Gebeyehu, S. & Samways, M.J. (2002) Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa), *Biodiversity and Conservation*, **11**, 283-304.

Gebeyehu, S. & Samways, M.J. (2006) Conservation refugium value of a large mesa for grasshoppers in South Africa, *Biodiversity and Conservation*, **15**, 717-734.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness, *Ecology Letters*, **4**, 379-391.

Guido, M. & Gianelle, D. (2001) Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area, *Acta Oecologia*, **22**, 175-185.

Hayes, G.F. & Holl, K.D. (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California, *Conservation Biology*, **17**, 1694-1702.

Heikkinen R.K. (1996) Predicting patterns of vascular plant species richness with composite variables: a meso-scale study in Finnish Lapland, *Vegetatio*, **126**, 151-165.

Hewitt, J.E., Thrush, S.E., Halliday, J. & Duffy, C. (2005) The importance of small-scale habitat structure for maintaining beta-diversity, *Ecology*, **86**, 1619-1626.

Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude, *Biological Reviews*, **80**, 489-513.

Hunter, Jr., M.L. (2005) A mesofilter conservation strategy to complement fine and coarse filters, *Conservation Biology*, **19**, 1025-1029.

Ingham, D.S. & Samways, M.J. (1996) Application of fragmentation and variegation models to epigaeic invertebrates in South Africa, *Conservation Biology*, **10**, 1353-1358

Joern, A. (1982) Vegetation structure and microhabitat selection in Grasshoppers (Orthoptera, Acrididae), *The Southwestern Naturalist*, **27**, 197-209.

Joern, A. (2004) Variation in Grasshopper (Acrididae) densities in response to fire frequency and Bison grazing the Tallgrass Prairie, *Environmental Entomology*, **33**, 1617-1625.

Joern, A. (2005) Disturbance by fire frequency and Bison grazing modulate grasshopper assemblages in Tallgrass Prairie, *Ecology*, **86**, 861-873.

Kemp, W.P., Harvey, S.J. & O'Neill, K.M. (1990) Patterns of vegetation and grasshopper community composition, *Oecologia*, **83**, 299-308.

Loaiza, V., Jonas, J.L. & Joern, A. (2011) Grasshoppers (Orthoptera: Acrididae) select vegetation patches in local-scale responses to foliar nitrogen but not phosphorus in native grassland, *Insect Science*, **18**, 533-540.

McIntyre, S. & Barrett, G.W. (1992) Habitat variegation, an alternative to fragmentation, *Conservation Biology*, **6**, 146-147.

Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs, *Ecology*, **92**, 2285-2298.

Mucina, L. & Rutherford, M.C. (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.

Oliver, I., Holmes, A., Dangerfield, J.M., Gillings, M., Pik, A.J., Britton, D.R., Holley, M., Montgomery, M.E., Raison, M., Logan, V., Pressey, R.L. & Beattie, A.J. (2004). Land systems as surrogates for biodiversity in conservation planning, *Ecological Applications*, **14**, 485-503.

PRIMER-E (2008) PERMANOVA and PRIMER 6. PRIMER-E, Lutton.

Pryke, J.S. & Samways, M.J. (2010) Significant variables for the conservation of mountain Invertebrates, *Journal of Insect Conservation*, **14**, 247-256.

Pryke, J.S. & Samways, M.J. (2012) Conservation management of complex natural forest and plantation edge effects, *Landscape Ecology*, **27**, 73-85.

Richardson, D.M. (2012) Conservation biogeography: what's hot and what's not? *Diversity and Distributions*, **18**, 319-322.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. & Yan, X. (2004) Effectiveness of the global protected area network in representing species diversity, *Nature*, **428**, 640-643.

Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates, *Annual Review of Ecology, Evolution, and Systematics*, **38**, 713-737.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, H., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100, *Science*, **287**, 1770-1774.

Samways, M.J. (1990) Land forms and winter habitat refugia in the conservation of montane grasshoppers in southern Africa, *Conservation Biology*, **4**, 375-382.

Samways, M.J. (1997) Conservation biology of Orthoptera. *The Bionomics of Grasshoppers, Katydids and their Kin* (ed. by S.K. Gangwere, M.C. Muralirangan and M. Muralirangan), pp. 481-487. CAB International, UK.

Samways, M.J. & Moore, S.D. (1991) Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa, *Biological Conservation*, **57**,117-137.

Samways, M.J. & Kreuzinger, K. (2001) Vegetation, ungulate and grasshopper interactions inside vs. outside and African savanna game park, *Biodiversity and Conservation*, **10**, 1963-1981.

Samways, M.J. & Sergeev, M.G. (1997) Orthoptera and landscape change. *The Bionomics of Grasshoppers, Katydids and their Kin* (ed. by S.K. Gangwere, M.C. Muralirangan and M. Muralirangan), pp. 147-162. CAB International, UK.

Sarkar, S., Justus, J., Fuller, T., Kelley, C., Garson, J. & Mayfield, M. (2005) Effectiveness of environmental surrogates for the selection of conservation area networks, *Conservation Biology*, **19**, 815-825.

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S. (2006) Biodiversity conservation planning tools: present status and challenges for the future, *Annual Reviews on Environment and Resources*, **31**, 123-159.

Tainton, N.M. & Mentis, M.T. (1984) Fire in grassland. *Ecological effects of fire in South African Ecosystems* (ed. by P. de V Booysen and N.M. Tainton), pp 115-147. Springer-Verlag, Berlin.

Telfer, M.G. & Hassall, M. (1999) Ecotypic differentiation in the grasshopper *Chorthippus brunneus*: life history varies in relation to climate, *Oecologia,* **121**, 245-254.

ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO reference manual and user's guide to Canoco for windows: software for Canonical community ordination (version 4.5).* Microcomputer Power, Ithaca.

Van Wingerden, W.K.R.E., Musters, J.C.M. & Maaskamp, F.I.M. (1991) The influence of temperature on the duration of eggs development in the West European grasshoppers (Orthoptera: Acrididae), *Oecologia*, **87**, 417-423.

Van Wingerden, W.K.R.E., Van Kreveld, A.R. & Bongers W. (1992) Analysis of species composition and abundance of grasshoppers (Orth., Acrididae) in natural and fertilized grasslands, *Journal of Applied Entomology*, **113**, 138-152.

Wessels, K.J., Freitag, A.S. & Van Jaarsveld, A.S. (1999) The use of land facets as biodiversity surrogates during reserve selection at a local scale, *Biological Conservation*, **89**, 21-38.

Wettstein, W. & Schmid, B. (1999) Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers, *Journal of Applied Ecology*, **36**, 363-373.

Willot, S.J. (1997) Thermoregulation in four species of British grasshoppers (Orthoptera: Acrididae), *Functional Ecology*, **11**, 705-713.

Chapter 5

Differential behavioural responses to rockiness in a landscape can help explain butterfly dispersion patterns

Abstract

Community patterns can be partially explained by defining the influential ecological parameters. Understanding how and why various species respond to various habitat resources, in turn, can optimise our conservation strategies. Furthermore, behaviour can contribute significantly to predicting the presence or absence of a species under certain habitat conditions. Evidence suggests a measureable interaction between higher rock exposure in a landscape and butterfly species richness and composition in Afro-montane grasslands. Here I set out to explain this interaction by measuring the behavioural responses of an Afro-montane butterfly assemblage towards rocks. I sampled the butterfly assemblage across three levels of rockiness in the landscape, as well as the different behavioural traits exercised at sites within each of these rocky categories. I then analysed the influence of rockiness on assemblage composition, and whether there were significant differences in behavioural traits of this assemblage to the rockiness categories. I also explored which species are responsible for driving differential behavioural responses in each rockiness category. Rockiness had a great influence on butterfly assemblage composition, especially between the extreme rockiness categories of high and low rockiness. Furthermore, high rockiness areas had significantly more behavioural events, and were more often associated with behaviours associated with physical utilisation of rocks and agonistic interaction. These behaviours were also species-specific, where a certain sub-assemblage of species were specialised for such rocky conditions. I then argue that the butterfly assemblage differentially responded to rockiness in the landscape as the different species use these rocks as a utility habitat resource. Collectively, the different behavioural responses of species to these rocky areas determine the dispersion patterns observed for this butterfly assemblage across a grassland landscape. These results emphasise the conservation importance of including rocky areas in local protected area and conservancy designs.

Introduction

Ecological parameters can help explain community patterns (Gilbert & Singer 1975), with insect assemblages, for example, often responding to a variety of environmental conditions (Jeanneret *et al*. 2003). These variables include elevation and topographical heterogeneity (Mac Nally *et al*. 2003; Gutiérrez Illán *et al*. 2010), land cover heterogeneity (Kerr *et al*. 2001), higher plant species richness (Jeanneret *et al*. 2003; Casacci *et al*. 2011), and vegetation composition and structure (Grill *et al*. 2005). Some species are often inherently associated with specific environmental conditions, which is why they are typically not uniformly distributed across a heterogeneous environment (Knapton 1985; Daily *et al*. 1991; Fleishman & Murphy 1999; Fleishman *et al*. 2001; Dover *et al*. 2011a). This makes predicting the composition of assemblages across a landscape all the more complex. For example, butterflies are known to have differential resource-based life history strategies, which mean that theoretically butterfly species can respond to multiple consumable and non-consumable resources, which are often unevenly distributed across a landscape (Dennis 2010). Thus, at a local scale, some species are more localized to certain biotopes (specialists), with others being more vagile (generalists) (Dover & Settele 2009; Dennis 2010).

The differential response of butterflies to landscape configuration has consequences for the conservation of this taxon (Wood & Samways 1991; Dover & Settele 2009). For example, Steffan-Dewenter & Tscharntke (2000) showed how certain specialist butterfly species negatively responded to habitat fragmentation, thus stressing the importance of having large tracks of calcareous grasslands protected in Germany. This means that there is value in knowing which resources within a landscape are associated with a butterfly assemblage, so as to include such variables in conservation planning initiatives (Shreeve & Dennis 2011). Indeed, delineating ecosystem features which are associated with a diversity of species, or mesofilters (Hunter 2005), would set important departure points in configuring a landscape design for optimal butterfly conservation in a changing world (Dover & Fry 2001; Dover *et al*. 2011b; Shreeve & Dennis 2011).

The study of butterfly behaviour in particular has contributed to predicting the presence or absence of a species under certain habitat conditions (Shreeve 1984; Thomas 1984; New 1991; see also Stamps *et al*. 2005). For example, Shreeve (1984) showed that the presence of a butterfly within a certain microhabitat was congruent with its thermoregulatory needs. Therefore, to include studies of how butterflies behaviourally respond to differential

resource conditions in a landscape would prove vital in understanding assemblage dispersion patterns across space and time (Shreeve & Dennis 2011). In fact, behavioural studies can contribute significantly towards conservation biology, since it can reveal the specific habitat requirements needed for a species, and subsequently how to optimally select a reserve (Sutherland 1998; Turlure *et al*. 2011).

There is a measureable interaction between higher rockiness within a landscape and butterfly species richness and composition in Afro-montane grasslands (Chapter 2). In turn, this suggests that we can use rockiness within a patch as a possible mesofilter for conservation of this taxon. However, the reason why butterflies would respond to such an abiotic variable in this grassland landscape is still to be explored. Dennis & Sparks (2005) showed how an ecosystem element, molehills, can greatly influence territorial butterfly behaviour in a landscape. Their study specifically emphasised the significance of micro-landform complexity as an important, and often overlooked, non-consumable or utility habitat resource for some butterflies (see Dennis 2010). Therefore, I hypothesise that certain butterfly species are responding to rocks in a landscape as a critical utility resource of their habitat, and that this response will be evident in their behaviour towards this physical ecosystem feature. In view of this, I examine the composition and behaviour of a butterfly community within a grassland landscape which differs in percentage rock exposure, and how observed behavioural traits might influence species dispersion patterns at the meso-scale.

Methods

Study area

The study was conducted within the 16 000 ha Merensky Forestry estate at Weza, near Kokstad, KwaZulu-Natal, South Africa. Around 4 200 ha are semi-natural open spaces, the remainder being commercial forestry. The open spaces lie mostly within the endangered Midlands Mistbelt Grassland vegetation type (Mucina & Rutherford 2006). The endangered status of this vegetation type is mainly driven by large forestry plantations in the area. The dominant grass is *Themeda triandra* Forssk. All selected sites are classified as semi-natural, as all were annually burned by forestry management over >6 decades. This frequency produces a dense productive grassland (Tainton & Mentis 1984), which equates to the natural

burning regime in the area of between one and ten ground lightning flashes $km^{-2}yr^{-1}$ (Edwards 1984). The geology is sand and siltstones from the Ecca group. Weathered resistant dolerite dykes are also present. The maximum height of the mountains is 2 200 m a.s.l., above an undulating landscape with minimum elevation of 900 m a.s.l.

This is a summer rainfall region, where most precipitation occurs between November and March. Annual precipitation varies around 1000 mm per annum in the low lying areas, to 1500 mm on the mountain peaks. Mean daily maximum temperature ranges from 17.6°C in June to 26°C in January. Mean daily minimum temperatures range from 0.1°C in June to 13.4°C in January.

Environmental variables

Eighteen sites were selected (see Fig. 2.1, Chapter 2). To calculate percentage rockiness of each site, a total of four 50 m transects were placed within each site, each transect being 15 m away from another (204 points per site). Percentage rockiness was then measured in two ways: 1) when rocks were touched by the pin (any rock greater than 10 cm in diameter), they were added and then divided by the total number of hits; 2) a metal stake was inserted in the ground every 5 m on each transect, giving 40 measurements per site, which serves as a composite indicator of surface rockiness (Stohlgren & Bachand 1997). This was done to ensure correct classification of the habitat as rocky, and not just a rocky outcrop within a non-rocky matrix. Elevation and aspect were measured on site with a handheld GPS (GPS 72, Garmin International, Inc.).

Butterfly assemblage sampling

Butterflies were sampled twice, in January and April 2011, to encompass the peak flight season. They were sampled within a 50 m radius from the middle point of each of the 18 sites used for the environmental variables measurements. This was conducted by two observers facing opposite directions. Each observation unit was 30 min, and replicated over three different days, at three different times of the day, making 90 min search time per person per site (3 hr total per site). In total, 96 hours was spent collecting these butterfly data. Sampling was between 09h00 and 15h00, on warm or hot days (average temperature of 30.2°C for January counts, and 24.7°C for April counts) with <5% cloud cover. Butterflies not

recognised on the wing were caught with a net, and identified in the field. To avoid pseudoreplication, sites of higher rockiness were interspersed with those of lower rockiness across the study area, with the minimum distance between similar sites being 400 m. Nomenclature is according to Woodhall (2005). All sampling was done >30 m away from the pine forest edge, to reduce sampling bias due to edge effects (Pryke & Samways 2012).

Butterfly behaviour observations

Behaviour was observed for each of the eighteen sites by two observers, between 09h00 and 15h00, on warm or hot days in February 2012 (average temperature of 28.3°C (±2.4°C SD) with <5% cloud cover. A total of three hours was spent observing behaviour at each site, rendering a total of six hours of observation time per site. Behaviour recording started as soon as a butterfly entered a 50-m radius circle from the middle of each site, and ended when the butterfly left the circle. The following behavioural observations were recorded where possible: 1) patrolling, where a butterfly is flying low over the area, at slow speed, as if investigating or searching; 2) touring, the butterfly is flying high, and at high speed, over the area, without showing any tendency of searching or investigating; 3) resting, the butterfly is settled, with wings closed; 4) perching, the butterfly is settled with its wings exposed to the sun, actively responding to other flying insects by chasing them and then returning to the same spot or another spot in the near vicinity; 5) feeding, a butterfly is settled on a flowering plant with proboscis extended into the flower; 6) courting, a male chasing after a disinterested female across the whole sampling site, or when both then alight to mate; 7) intra-specific aggression, a male chases a conspecific male horizontally for a couple of seconds, or chases another male in a vertical upward swirl; 8) inter-specific aggression, a male chases another species (butterflies or other flying insects) horizontally, or chases them in a vertical upward swirl.

Statistical analysis

To ensure adequate taxon representation, sampling was conducted until the species accumulation curve near flattened (Gotelli & Colwell 2001) (Appendix B). To determine the influence of the measured environmental variables on species assemblage composition, a canonical correspondence analysis (CCA) was performed using CANOCO 4.5 (ter Braak &

Šmilauer 2002). Furthermore, to experiment what effect variable levels of rock exposure within a patch have on butterfly species composition in the habitat, I used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) in PRIMER 6 (PRIMER-E 2008). PERMANOVA results are reported as F- and *P*-values, where a significant p-value indicates a significant difference (at the 5% level) between levels (groups) of a studied factor. In addition, I also performed a canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003) for each of the vegetation correlates of rockiness in PRIMER 6 (PRIMER-E 2008). CAP allows visualization of patterns of community differences across certain treatments, and also whether the observed spread of a group is by chance alone through cross validation by 'leave-one-out' allocations (e.g. Messmer *et al* 2011). For these statistics, I categorized percentage rockiness as high rockiness (HR) (n = 6), medium rockiness (MR) (n = 6) and low rockiness (LR) (n = 6). All these categories were chosen as they represent a gradual increase in the rockiness values measured across the eighteen sites. Both PERMANOVA and CAP analyses were performed using Bray-Curtis similarity measures where data for each group were fourth-root transformed to reduce the weight of the common species (Anderson 2001).

To explore the butterfly behaviour associated to variable levels of rock exposure within a patch, I calculated the mean percentage incidence of each behavioural group per site. I then pooled percentage behavioural events form all six sites according to the three rocky categories used for the PERMANOVA and CAP analyses (HR, MR and LR). Then, to explore the contribution of these rocky categories on mean percentage behavioural events in a group, I made use of generalized linear models (GLZ) (McCulloch *et al*. 2008) followed by a post-hoc test in SAS Enterprise Guide 5.1 (SAS Institute, Inc.). Beforehand, the values for every behavioural group were tested for normality and their variances tested for homogeneity using a Shapiro-Wilk test, and tested for Poisson distribution through a Chi-squared goodness of fit test (Statistica Release 10, StatSoft, Inc.). As such, for the patrolling, touring, resting and feeding behaviour groups, each GLZ had a normal distribution and an identity-link function. Whereas for the perching, courting, intra-specific and inter-specific behaviour groups, GLZ's with a Poisson distribution and log-link function were used.

Furthermore, to examine which butterfly species were the main contributors to the different behavioural patterns observed across each rockiness category (according to the GLZ results), I constructed summary tables which indicate which species were more physically active within each rockiness category.

Results

Butterfly assemblage composition

A total of 47 butterfly species were observed. Variable levels of rockiness were influential in structuring this grassland butterfly community (Fig. 5.1). Specifically, rocky north-faces and rocky ridges had a unique assemblage as opposed to less rocky south facing slopes. Furthermore, there was a significant difference in butterfly assemblage composition across a three-way rockiness classification (F = 1.75, *P* = 0.012) (Table 5.1). Specifically, the high rocky areas had a significantly different assemblage composition than the low rocky areas (t = 1.59, *P* = 0.005) (Table 5.1). Consistent with the PERMANOVA pairwise test, was the CAP analysis which visualised this difference in butterfly assemblage composition between the two extreme rockiness sites (Fig. 5.2). CAP analysis suggested that a unique assemblage of species was especially associated with high rocky areas, as this category had a low misclassification error in ordination space (16.7%) (Fig. 5.2).
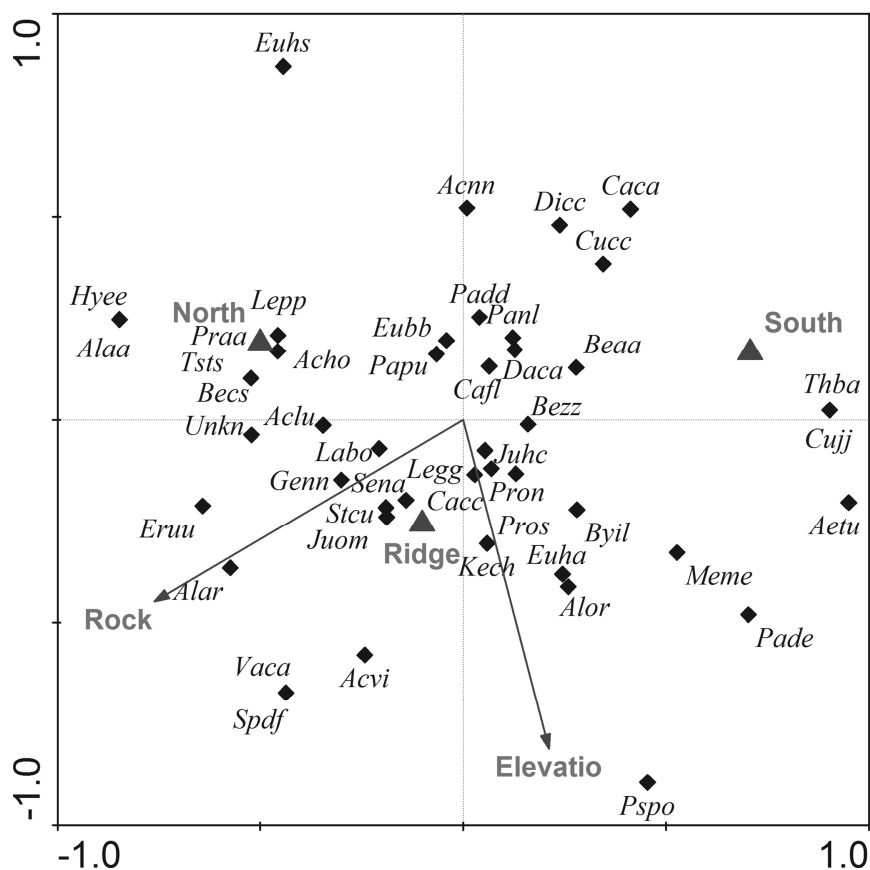
Figure 5.1 Canonical correspondence analysis (CCA) ordination for all recorded butterfly species and measured environmental variables. Aspect is labelled as North, South or Ridge (neutral). Rock is percentage rock exposure within a site. Full names for species abbreviations as in Appendix F

Table 5.1 PERMANOVA analysis of the influence of rockiness on butterfly species composition across all sites, as well as pairwise test of differences in assemblage composition between rockiness groups. HR, high rockiness; MR, medium rockiness; LR, low rockiness

	df	**Pseudo-F or t**	***P*-value**
Overall test	2	1.75	**0.012**
Pairwise tests			
HR*MR		1.11	0.264
HR*LR		1.59	**0.005**
MR*LR		1.22	0.127

Values in bold are significant at the 5% level
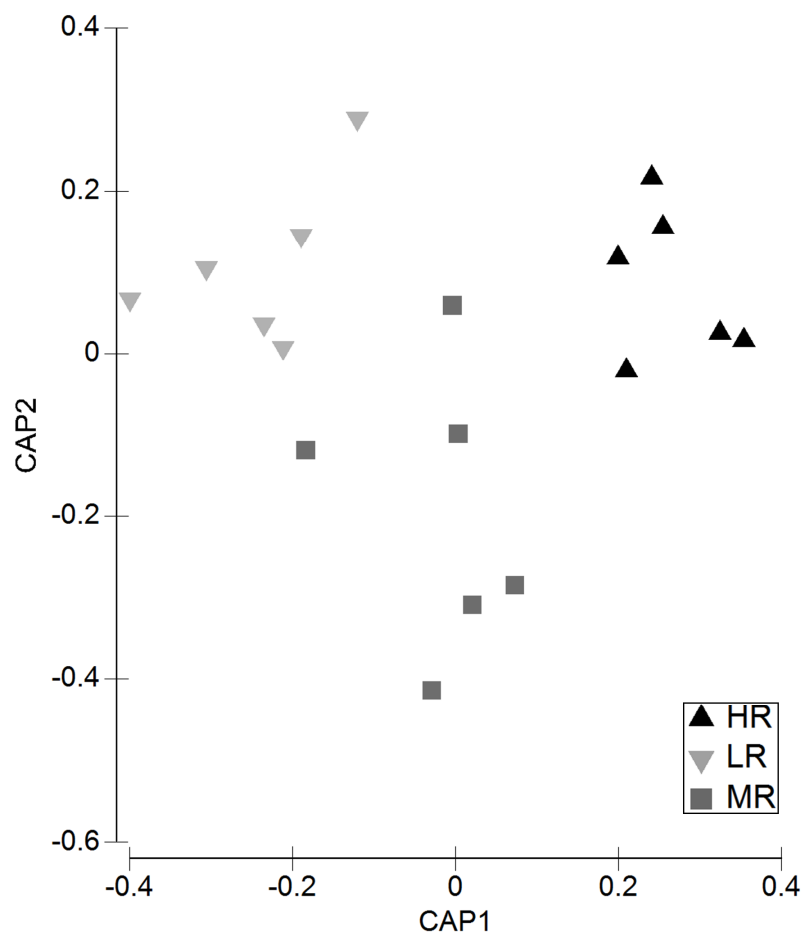
Figure 5.2 Canonical analysis of principal coordinates (CAP) ordination plot of butterfly assemblage data across the rockiness categories. HR, high rockiness; MR, medium rockiness; LR, low rockiness. Misclassification error for rockiness classes: HR = 16.7%; MR = 50.0%; LR = 33.3%

The behavioural events of 43 butterfly species were observed. Behavioural events were not equally distributed between the rockiness categories. High rocky sites (HR) had the most recorded behaviour events (761 events), followed by medium rocky sites (MR) (623 events), and low rocky sites (LR) (437 events). This was partially driven by abundance.

The mean percentage behavioural events within each recorded behaviour significantly differed across the rocky categories for touring (Wald 18.95, P <0.001), resting (Wald 11.48, P = 0.003), perching (Wald 23.34, P <0.001), courting (Wald 7.39, P = 0.025), intra-species aggression (Wald 10.60, P = 0.005) and inter-species aggression (Wald 9.35, P = 0.009) (Table 5.2). There were no significant difference in the percentage feeding (Wald 1.13, P = 0.568) and patrolling (Wald 0.89, P = 0.640) observations across the rockiness classes (Table 5.2).

Post-hoc results showed that high rocky areas (HR) significantly differed in mean percentage behavioural observations from both medium and low rocky areas for resting and perching behaviour (P <0.05) (Table 5.3). High rocky areas also showed more intra-specific aggression behaviour than low rocky areas, but not medium rocky areas (Table 5.3). In turn, both high and medium rocky areas had significantly more behavioural events recorded for perching and inter-specific aggression than low rocky areas. There was a significantly higher percentage touring behaviour in low rocky areas, as opposed to high and medium rocky areas (P <0.05) (Table 5.3).

Table 5.2 Generalized linear modelling (GLZ) of the behavioural events recorded within each behaviour group across a three-way rockiness classification

Behaviour	*df*	Wald Statistic	*P*-value
Patrol	2	1.13	0.568
Tour	2	18.95	**<0.001**
Rest	2	11.48	**0.003**
Perch	2	23.34	**<0.001**
Feed	2	0.89	0.640
Court	2	7.39	**0.025**
Intra-species Aggression	2	10.60	**0.005**
Inter-species Aggression	2	9.35	**0.009**

Values in bold are significant at the 5% level

n = 6

Table 5.3 Mean percentage behavioural events (±SE) for each behaviour group in high (HR), medium (MR) and low (LR) rocky sites

	Behaviour							
	Patrol	**Tour**	**Rest**	**Perch**	**Feed**	**Court**	**Intra**	**Inter**
HR	33.71 (4.40)	8.27^a (2.19)	13.85^a (1.81)	15.29^a (2.40)	18.00 (4.24)	3.64^a (1.65)	3.03^a (1.55)	4.21^a (2.36)
MR	38.94 (3.15)	17.61^a (5.05)	6.97^b (1.76)	9.49^b (4.46)	20.24 (5.65)	1.34^{bc} (0.84)	1.32^{ac} (1.15)	4.10^a (2.89)
LR	33.57 (5.48)	36.61^b (7.00)	6.04^b (2.24)	6.21^c (3.43)	14.08 (5.34)	1.79^{ac} (0.59)	0.43^{bc} (0.29)	1.26^b (0.83)

Within each behaviour group, different superscripts indicate significant differences of the means at the 5% level

n = 6

Table 5.4 Summary of species directly utilising rocks or plants (number of recorded events) in habitats with varying levels of rockiness

Species	Resting		Perching		
	Rock	Plant	Rock	Plant	Total
High Rockiness (HR)					
Precis octavia sesamus f. *natalensis*	24	15	40	16	**95**
Stygionympha wichgrafi	25	2	23	0	**50**
Stygionympha curlei	20	2	11	0	**33**
Actizera lucida	0	6	0	4	**10**
Lampides boeticus	2	2	1	3	**8**
Papilio demodocus demodocus	0	1	1	3	**5**
Gegenes niso niso	1	2	1	1	**5**
Eretis umbra umbra	2	0	1	2	**5**
Danaus chrysippus aegyptius	0	2	0	2	**4**
Precis octavia sesamus	0	0	2	0	**2**
Leptotes pirithous pirithous	0	1	0	0	**1**
Total	**74**	**33**	**80**	**31**	
Medium Rockiness (MR)					
Precis octavia sesamus f. *natalensis*	4	0	29	2	**35**
Stygionympha wichgrafi	3	0	10	0	**13**
Catacroptera cloanthe cloanthe	3	3	0	3	**9**
Aloeides aranda	0	0	9	0	**9**
Danaus chrysippus aegyptius	0	5	0	3	**8**
Cupidopsis cissus cissus	0	3	0	2	**5**
Actizera lucida	0	4	0	0	**4**
Catopsilia florella	0	1	0	2	**3**
Eurema brigitta brigitta	0	3	0	0	**3**
Belenois aurota aurota	0	1	0	0	**1**
Junonia hierta cebrene	0	0	0	1	**1**
Total	**10**	**20**	**48**	**13**	
Low Rockiness (LR)					
Leptotes pirithous pirithous	0	5	0	6	**11**
Gegenes niso niso	0	3	0	3	**6**
Danaus chrysippus aegyptius	0	2	1	2	**5**
Pseudonympha poetula	0	3	0	2	**5**
Cupidopsis cissus cissus	0	1	0	2	**3**
Papilio demodocus demodocus	0	1	0	2	**3**
Precis octavia sesamus f. *sesamus*	1	0	1	0	**2**
Belenois aurota aurota	0	0	0	2	**2**
Precis octavia sesamus f. *natalensis*	1	0	0	0	**1**
Total	**2**	**15**	**2**	**19**	

A total of eight species physically utilised the rocks to either rest or perch in high rocky areas, whereas in the medium rocky areas there were only four species utilising the rocks, and in the low rocky areas only two species utilising rocks. Two nymphalid butterfly species, *Precis octavia sesamus* f. *natalensis* and *Stygionympha wichgrafi* were responsible for driving the observed higher perching and resting behavioural events in higher and medium rocky areas (Table 5.4). In general, this was because these two species, as well as another nymphalid, *Stygionympha curlei*, were physically utilising the rocks to either rest or perch, more so than on plants. It was also clear, that the most active species in the low rocky areas differed from the ones in the higher and medium rocky areas, and, they used plants to either perch or rest. Also, there was more activity in the perching and resting behaviour groups under higher levels of rockiness.

Consistent with the resting and perching behaviour pattern, increased activity from *P. octavia sesamus* f. *natalensis* was also responsible for the higher percentage intra- and inter-specific agonistic behaviour observed at high and medium rocky sites, as opposed to low rocky sites (Table 5.5). This aggressive interaction in rocky areas is congruent with increased courting activity of this species. Overall, higher rockiness is more associated with agonistic species, as there was more agonistic interaction from a higher number of species at the higher rocky sites (Table 5.5).

Table 5.5 Summary of species interactive behaviour in habitats (number of recorded events) featuring varying levels of rockiness

Species	Courting	Aggressive Interaction		Total
		Intraspecific	Interspecific	
High Rockiness (HR)				
Precis octavia sesamus f. *natalensis*	24	27	35	**86**
Stygionympha wichgrafi	0	4	5	**9**
Papilio demodocus demodocus	6	1	2	**9**
Lampides boeticus	1	3	3	**7**
Leptotes pirithous pirithous	2	1	2	**5**
Gegenes niso niso	2	0	0	**2**
Danaus chrysippus aegyptius	0	0	1	**1**
Catopsilia florella	1	0	0	**1**
Leptotes pirithous pirithous	0	0	1	**1**
Total	**36**	**36**	**49**	

Medium Rockiness (MR)				
Precis octavia sesamus f. *natalensis*	6	6	11	**23**
Aloeides aranda	0	0	9	**9**
Stygionympha wichgrafi	1	2	3	**6**
Catopsilia florella	1	1	2	**4**
Catacroptera cloanthe cloanthe	0	0	2	**2**
Total	**8**	**9**	**27**	
Low Rockiness (LR)				
Gegenes niso niso	4	0	3	**7**
Pseudonympha poetula	0	1	2	**3**
Precis octavia sesamus f. *natalensis*	0	0	2	**2**
Catopsilia florella	1	0	0	**1**
Papilio demodocus demodocus	0	1	0	**1**
Aeropetes tulbaghia	1	0	0	**1**
Total	**6**	**2**	**7**	

Discussion

Utility resources in a habitat (non-consumable resources), such as substrate exposure, where a butterfly can rest or perch upon, can have a significant impact on how butterflies respond to a landscape (Dennis 2010). Furthermore, this response to resources will also be evident in their behaviour (Dover 1997; Dover & Fry 2001; Dennis 2010). However, very few studies have specifically studied butterfly behavioural response to substrates, and how this can aid in butterfly conservation strategies (Dennis *et al*. 2006). Here, I showed there are specific behavioural responses of butterflies to varying levels of rock exposure in a habitat, and that this differential behavioural response can help explain the dispersion patterns of butterflies across an Afro-montane grassland landscape.

Butterfly utilisation of habitat resources

Overall, there was a strong trend for certain butterfly species to be highly associated to sites of higher rock exposure as measured at this meso-scale. There is a known association of some butterfly species to rock features, e.g. rocky outcrops, as well as being present in high densities at such rocky features (Gutiérrez 1997). It is often suggested that such a rock-butterfly association exists as there is congruence between rocky landscape features and

certain vegetation that might include butterfly feeding plants (Gutiérrez 1997; Terblanche *et al*. 2003). For example, Terblanche *et al*. (2003) suggested that the reason why a lycaenid species, *Chrysoritis aureus*, was associated with rocks in a South African grassland, was that the host plant of this butterfly could be associated with greater rock exposure in the patch. Of course, utility resources can be closely associated with consumable resources (Dennis 2010). Furthermore, we know that rocky areas coincide with higher plant species richness in certain Afro-montane grasslands (Chapter 2). This means that few plant species in this grassland landscape are not associated with rocky areas, as opposed to less rocky areas (Chapter 3). This suggests that a higher diversity of host plants may be present at these rocky sites, and in turn can, at least in part, explain the observed butterfly assemblage compositional differences across this landscape. In other words, there could be more specialist butterfly species selecting nectar sources from the wider variety of plants present in the rocky patches, whereas the less rocky and less plant diverse areas have more generalist species. However, although some butterfly species will only be present where their specific host plant is present (e.g. Krauss *et al*. 2004), the distribution of specific butterfly host plants do not necessarily limit the distribution of the majority of butterflies across a landscape (Dennis & Shreeve 1991). Also, plant diversity does not necessarily directly influence butterfly diversity across space, however, their distribution is likely to be driven by a similar environmental variable (Hawkins & Porter 2003). Here, I argue that a high level of rock exposure in a landscape is such an environmental variable.

There was more behavioural activity recorded in the high rocky areas than the low rocky areas. There were also two distinct assemblages associated with high and low rocky areas. Thus, the butterfly assemblage in the high rocky areas was overall more active in some aspects of their behaviour. However, here I show that this manifestation was not a function of a higher percentage of feeding events in higher rocky areas, where there was higher host plant diversity. On the other hand, I found that mean percentage behavioural events specifically associated with physical utilisation of rocks for resting and perching, was significantly higher in the rockier areas. The differential response in the higher number of behaviour events in rockier areas is therefore an artefact of this non-consumable resource as opposed to the consumable resource (flora) associated with it. Moreover, this response was species specific, where a higher diversity of species was directly utilising rocks in the rockier landscape, whereas others did not utilise the rocks at all. In turn, this suggests a specialist response of species to rocks in the landscape. This suggests that the dispersion pattern for the butterfly

assemblage observed in rockier areas is likely not associated to a plant-rockiness interaction, but rather that the rockiness *per se* was used as a particular resource by a certain component of the assemblage (used as a utility resource) (*sensu* Dennis 2010).

Rocks and resting behaviour

In this study, three Nymphalidae species were predominantly driving the observation of increased resting behaviour on rocks: *Precis octavia sesamus* f. *natalensis*, *Stygionympha wichgrafi* and *S. curlei*. Firstly, this indicates a familial response to resting on rocks, and secondly, a further sub-familial response, where two closely related satyrines, *S. wichgrafi* and *S. curlei*, showed a close association to using rocks in this grassland. These two satyrines were responsible for 45 out of 74 rock resting behavioural events recorded in the high rocky areas. The question remains why these closely related butterflies would select this particular substrate to rest upon. Woodhall (2005) observed that satyrines are usually weak fliers, which is why they settle often. Furthermore, Brakefield and Reitsma (1991) showed how another satyrine genus in Africa, *Bicyclus*, avoids visually-hunting predators through resting on objects with a brown coloured background. Butterflies can discern colours, and, they use this ability to cue a certain behavioural response pertaining to their life-history strategy (Vaidya 1969). The rocks in this grassland provide a brown coloured background (see Fig. 5.3). This suggests that these *Stygionympha* species show a positive cryptic response to rocks as they move across the landscape.

Resting behaviour on rocks is also closely linked to butterfly thermoregulation (Clench 1966; Masters *et al*. 1988). Indeed, butterflies are heliotherms, and will select certain substrates to aid in their thermoregulatory needs (Dennis 2010). Clench (1966) suggested that butterflies may use rocks for thermoregulation through direct body contact, especially so earlier and later in the day, when the ambient temperature is lower than the temperature of the rocky surface. In contrast, Masters *et al*. (1988) showed that a Nymphalidae species, *Danaus plexippus*, can also use rocky surfaces for sun-minimizing behaviour, i.e. to help prevent the butterfly form overheating under warm ambient conditions. *P. octavia sesamus* f. *natalensis*, a bright orange Nymphalidae species, which also frequently rested on rocks, could be showing a positive sun-minimizing response to rocks at certain times of the day. Although this was not explicitly tested here, this explanation for their rock resting behaviour in summer temperatures is more likely than them responding to rocks for crypsis.

Essentially, we know that certain species utilise bare rock for a variety of thermoregulatory behaviours. The significantly higher resting behavioural events recorded in higher rocky areas strengthens this assumption. This is a highly specialised behaviour towards rocks in landscape, and emphasises the significance of rocky areas in influencing species dispersion patterns.

Figure 5.3 A *Stygionympha curlei* individual resting on a rock

Rocks, territorial behaviour, and mate-locating

Territorial behaviour or 'site defense' is known to be associated with specific behavioural events such as patrolling and perching (Baker 1972; Dennis & Shreeve 1988; Rutowski 1991; Fischer & Fiedler 2001). In addition, butterflies often behaviourally respond to visual cues in their territory, such as rocks, stony soils and bare-ground, which helps them exercise such

territorial behaviour activities (Bitzer & Shaw 1979; Knapton 1985; Daily *et al*. 1991). This can also be a familial response, for example, Tiple *et al*. (2010) reported how perching behaviour in the Nymphalidae, and hence territorial behaviour, was closely associated with rock faces. Here, I also show how the Nymphalid species, *P. octavia sesamus* f. *natalensis* and *S. wichgrafi*, positively responded to perching specifically on rocks in areas of higher rockiness. In addition, *P. octavia sesamus* f. *natalensis* had by far more agonistic behavioural events towards conspecifics and other butterfly species in this rockiness category. This species even chased other flying insect species, such as dragonflies (CJ Crous, personal observation). Moreover, males of *P. octavia sesamus* f. *natalensis* showed the highest incidence of courting behaviour. For another nymphaline, *Hypolimnas bolina*, it was suggested that an optimised strategy to find suitable females, was to perch for an extended time of the day, and then inspect every bypassing flying butterfly individual (Kemp 2001). Collectively, this all points to males of *P. octavia sesamus* f. *natalensis* being highly territorial at rockier sites as a result of searching for potential female mates.
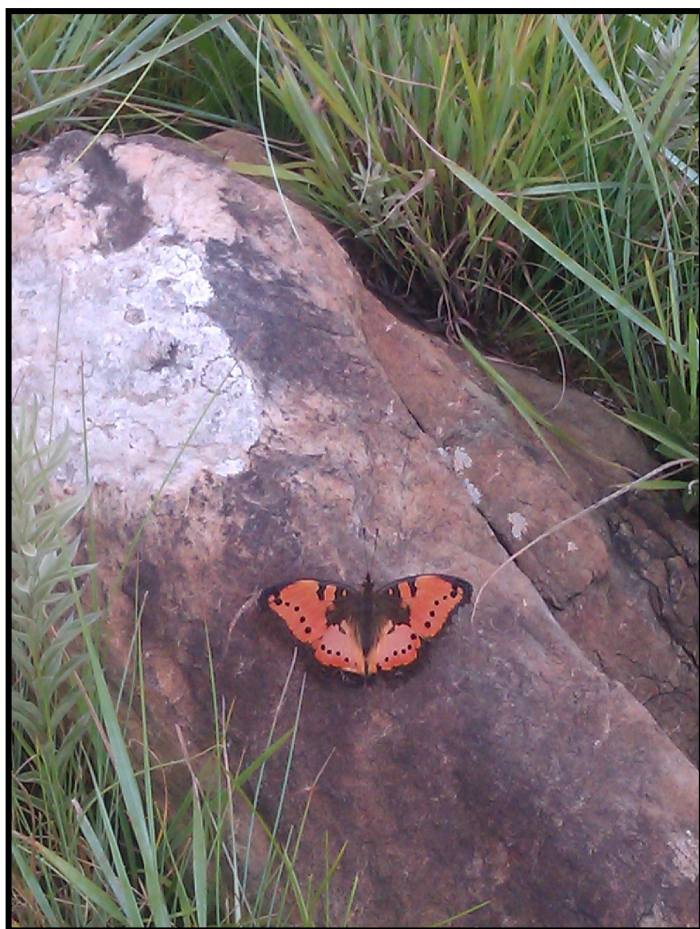
Figure 5.4 A *Precis octavia sesamus* f. *natalensis* individual perching on a rock as a vantage point to attack another butterfly individual.

The CCA ordination indicated that landscape landmarks, such as ridges, could be a confounding factor in this result of higher mate-locating behaviour at high rocky sites due to possible hilltopping behaviour. However, here I show that *P. octavia sesamus* f. *natalensis*, which can be quite common across the landscape, is specifically exercising more courting behaviour in the presence of higher rock exposure. Daily *et al.* (1991) attributed the usage of certain landmarks in a landscape, such as roads (open areas devoid of vegetation), to be optimal vantage points for *Oneis chryxus* to find passing females. Thus, although *P. octavia sesamus* f. *natalensis* do aggregate on hilltops, the rocky nature of these hilltops is of great importance for males of this species as a vantage point to help exert agonistic and courting behaviour (*sensu* Dennis & Shreeve 1988; see also Lawrence & Samways 2002) (see Fig. 5.4).

An important principle in mate-locating is that butterflies often select sites in a habitat that ensure optimal flight conditions and therefore optimised mate location (Dennis 2010). The duality of rocks as a utility or non-consumable resource for *P. octavia sesamus* f. *natalensis* becomes apparent. Not only do they use rocks as vantage points for either attacking other males or courting with females, but they also use the rocks for ensuring optimal thermoregulation. This use of a micro-landform could therefore aid in their flight performance (Dennis & Sparks 2005), and has an added advantage for this species pertaining to hours spent mate-locating and territory defence. This was also found for dragonflies in South Africa (McGeoch & Samways 1991).

Modelling invertebrate populations, Scott (1977) reported on the significant effect that mate-locating territorial behaviour can have on excluding other competitive species in a habitat. He specifically found that two species with dissimilar mate-locating efficiencies would not be able to occupy the same niche. Furthermore, Pinheiro (1990) found that inter-specific aggressive interaction between two Papilionidae species lead to non-overlapping territories between the two species. Bearing in mind that most agonistic behaviour recorded was at the high rocky sites, specifically by the species *P. octavia sesamus* f. *natalensis*, I believe that the significantly different assemblages found between the two extreme rocky categories (low and high) may be a function of competitive exclusion.

The ability of Nymphalid species to protect their territory from intrusion by other male butterflies is well known (Baker 1972). Kunte (2008) also showed how the removal of nymphalines in the *Anartia* genus from the community significantly increased the butterfly diversity of the area. He attributed this diversity increase to *Anartia* species outcompeting

other members of the community for nectar, and upon its exclusion, other butterfly species could utilise this resource more readily. Here, *P. octavia sesamus* f. *natalensis* was mostly active in the rockier sites, specifically exercising territorial behaviour. However, other species also exerted similar agonistic behaviour at these sites, although markedly less so. This suggests that not all species were excluded by the territorial behaviour of *P. octavia sesamus* f. *natalensis*. Indeed, where an area has a dominant species defending its territory and another species alights in the area, the territory resident may not see the intruder or is engaged with courting a female (Baker 1972). The newly settled species then starts defending its 'new' territory, but could eventually lose against the dominant resident species and leave the area (Baker 1972; Davies 1978). This is also known as the 'resident wins, intruder retreats' principle, but exceptions do exist (Davies 1978). Collectively, it seems that the more aggressive species are associated with rockiness in this study as they probably have similar territorial behavioural efficiencies than *P. octavia sesamus* f. *natalensis*, whereas other species which have low site tenacity, and no site defensive behaviour, are excluded from these sites through inter-specific agonistic behaviour (*sensu* Scott 1977, Rutowski 1991). Essentially, the specialised territorial adaptation of *P. octavia sesamus* f. *natalensis* in utilising rocks as a vantage point for inter-specific agonistic behaviour can therefore be seen as influencing the dispersion patterns in this butterfly assemblage across this landscape.

Conclusion

Butterflies exploit finer-scale landscape structural features to help execute specific behaviour traits (Dennis & Sparks 2005). Indeed, the structural components of a habitat, or non-consumable resources, are of great importance to butterflies in fulfilling critical life-history strategies (Dennis 2004). In this study, I hypothesised that certain butterfly species are responding to rocks in the landscape as a critical non-consumable resource of their habitat, and that this response will be evident in their behaviour towards this physical ecosystem feature. I have shown that this Afro-montane grassland butterfly assemblage does indeed behaviourally respond to rockiness in the landscape, with rocks therefore being a crucial utility resource in this landscape, which will be an important tool for conservation of butterflies (Dennis *et al*. 2006; Dennis 2010). This is also an important finding pertaining to understanding butterfly biology (Dennis 2004), as this result shows the direct exploitation of

rocks by certain butterflies. It also emphasises that a butterfly species can be present in a landscape for more reasons than just feeding. Moreover, it was clear that this response to rocks is highly species-specific. This differential behavioural response of species to rocky areas can be seen as a major contribution to the dispersion patterns observed for this butterfly assemblage across this grassland landscape. Whether other factors, such as roosting underneath rocks, are also influencing species presence under such rocky conditions, needs further exploration. Therefore, to conserve a diverse array of butterfly species, we need to pursue a resource-based conservation strategy (Dennis 2010). Consequently, for Afromontane grasslands, it is critical to include rocky areas in protected areas or in conservancy designs. In fact, rocky areas are an important mesofilter in this grassland type (Chapter 2). However, it is clear from the assemblage differences, that the less rocky matrix must also be included. Thus, for butterflies, we need to conserve a rocky gradient within a landscape.

References

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance, *Austral Ecology*, **26**, 32–46.

Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology, *Ecology*, **84**, 511-525.

Baker, R.R. (1972) Territorial behaviour of the Nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). *Journal of Animal Ecology*, **41**, 453-469

Bitzer, R.J. & Shaw, K.C. (1979) Territorial behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). *Journal of Research on the Lepidoptera*, **18**, 36-49

Brakefield, P.M. & Reitsma, N. (1991) Phenotypic plasticity, seasonal climate and the population biology of *Bicyclus* butterflies (Satyridae) in Malawi. *Ecological Entomology*, **16**, 291-303

Casacci, L.P., Witek, M., Barbero, F., Patricelli, D., Solazzo, G., Balletto, E. & Bonelli, S. (2011) Habitat preferences of *Maculinea arion* and its *Myrmica* host ants: implications for habitat management in Italian Alps. *Journal of Insect Conservation*, **15**, 103-110

Clench, H.K. (1966) Behavioral thermoregulation in butterflies. *Ecology*, 47, 1021-1034

Daily, G.C., Ehrlich, P.R. & Wheye, D. (1991) Determinants of spatial distribution in a population of the subalpine butterfly *Oneis chryxus*. *Oecologia*, **88**, 587-596

Davies, N.B. (1978) Territorial defence in the Speckled Wood Butterfly (*Pararge aegeria*): the resident always wins. *Animal Behaviour*, **26**, 138-147

Dennis, R.L.H. (2004) Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. *Ecological Entomology*, **29**, 744-752

Dennis, R.L.H. (2010) *A resource-based habitat view for conservation: butterflies in the British landscape*. Wiley-Blackwell, UK

Dennis, R.L.H. & Shreeve, T.G. (1988) Hostplant-habitat structure and the evolution of butterfly mate-locating behaviour. *Zoological Journal of the Linnean Society*, **94**, 301-318

Dennis, R.L.H. & Shreeve, T.G. (1991) Climatic change and the British butterfly fauna: opportunities and constraints. *Biological Conservation*, **55**, 1-16

Dennis, R.L.H., Shreeve, T.G. & van Dyck, H. (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation*, **15**, 1943-1966

Dennis, R.L.H. & Sparks, T.H. (2005) Landscape resources for the territorial Nymphalid butterfly *Inachis io*: microsite landform selection and behavioural reponses to environmental conditions. *Journal of Insect Behavior*, **18**, 725-242

Dover, J.W. (1997) Conservation headlands: effects on butterfly distribution and behaviour. *Agriculture, Ecosystems and Environment*, **63**, 31-49

Dover, J.W. & Fry, G.L.A. (2001) Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. *Entomologia Experimentalis et Applicata*, **100**, 221-233

Dover, J. & Settele, J. (2009) The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation*, **13**, 3-27

Dover, J.W., Rescia, A., Fungariño, S., Fairburn, J., Carey, P., Lunt, P., Arnot, C., Dennis, R.L.H. & Dover, C.J. (2011a) Land-use, environment, and their impact on butterfly populations in a mountainous pastoral landscape: individual species distribution and abundance. *Journal of Insect Conservation*, **15**, 207-220

Dover, J.W., Warren, M.S. & Shreeve, T.G. (2011b) 2010 and beyond for Lepidoptera. *Journal of Insect Conservation*, **15**, 1-3

Edwards, D. (1984) Fire regimes in the biomes of South Africa. *Ecological effects of fire in*

South African Ecosystems (ed. by P. de V Booysen and N.M. Tainton), pp 19-37. Springer-Verlag, Berlin.

Fischer, K. & Fiedler, K. (2001) Resource-based territoriality in the butterfly *Lycaena hippothoe* and environmentally induced behavioural shifts. *Animal Behaviour*, **61**, 723-732

Fleishman, E., Mac Nally, R., Fay, J.P. & Murphy, D.D. (2001) Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. *Conservation Biology*, **15**, 1674-1685

Fleishman, E. & Murphy, D.D. (1999) Patterns and processes of nestedness in a Great Basin butterfly community. *Oecologia*, **119**, 133-139

Gilbert, L.E. & Singer, M.C. (1975) Butterfly ecology. *Annual Review of Ecology and Systematics*, **6**, 365-397

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness, *Ecology Letters*, **4**, 379-391

Grill, A., Knoflach, B., Cleary, D.F.R. & Kati, V. (2005) Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. *Biodiversity and Conservation*, **14**, 1281-1300

Gutierrez, D. (1997) Importance of historical factors on species richness and composition of butterfly assemblages (Lepidoptera: Rhopalocera) in a northern Iberian mountain range. *Journal of Biogeography*, **24**, 77-88

Gutiérrez Illán, J., Gutiérrez, D. &Wilson, R.J. (2010) Fine-scale determinants of butterfly species richness and composition in a mountain region. *Journal of Biogeography*, **37**, 1706-1720

Hawkins, B.A. & Porter, E.E. (2003). Does herbivore diversity depend on plant diversity? The case of California butterflies. *The American Naturalist*, 161, 40-49

Hunter, Jr., M.L. (2005) A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology*, **19**, 1025-1029

Jeanneret, Ph., Schüpbach, B. & Luka, H. (2003) Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. *Agriculture, Ecosystems and Environment*, **98**, 311-320

Kemp, D.J. (2001) Investigating the consistency of mate-locating behavior in the territorial butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae). *Journal of Insect Behavior*, **14**, 129-147

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences USA*, **98**, 11365-11371

Knapton, R.W. (1985) Lek structure and territoriality in the chryxus arctic butterfly, *Oneis chryxus* (Satyridae). *Behavioral Ecology and Sociobiology*, **17**, 389-395

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2004) Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. *Biological Conservation*, **120**, 355-361

Kunte, K. (2008) Competition and species diversity: removal of dominant species increases diversity in Costa Rican butterfly communities. *Oikos*, **117**, 69-76

Lawrence, J.M. & Samways, M.J. (2002) Influence of hilltop vegetation type on an African butterfly assemblage and its conservation. *Biodiversity and Conservation*, **11**, 1163-1171

Masters, A.R., Malcolm, S.B. & Brower, L.P. (1988) Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. *Ecology*, **69**, 458-467

Mac Nally, R., Fleishman, E., Fay, J.P. & Murphy, D.D. (2003) Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. *Biological Conservation*, **110**, 21-31

McCulloch, C.E., Searle, S.R. & Neuhaus, J.M. (2008) *Generalized, linear, and mixed models*, 2nd edition. Wiley, USA

McGeoch, M.A. & Samways, M.J. (1991) Dragonflies and the thermal landscape: implications for their conservation (Anisoptera). *Odonatologica*, **20**, 303-320

Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs, *Ecology*, **92**, 2285-2298

Mucina L and Rutherford MC (eds) (2006) The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria

New, T.R. (1991) *Butterfly conservation*. Oxford University Press, Australia

Pinheiro, C.E.G. (1990) Territorial hilltopping behaviour of three Swallowtail butterflies (Lepidoptera, Papilionidae) in western Brazil. *Journal of Research on the Lepidoptera*, **29**, 134-142

PRIMER-E (2008) PERMANOVA and PRIMER 6. PRIMER-E, Lutton

Pryke, J.S. & Samways, M.J. (2012). Conservation management of complex natural forest and plantation edge effects. *Landscape Ecology*, **27**, 73-85

Rutowski, R.L. (1991) The evolution of mate-locating behaviour in butterflies. *The American Naturalist*, **138**, 1121-1139

Scott, J.A. (1977) Competitive exclusion due to mate searching behaviour, male-female emergence lags and fluctuation in number of progeny in model invertebrate populations. *Journal of Animal Ecology*, **46**, 909-924

Shreeve, T.G. (1984) Habitat selection, mate location, and microclimatic constraints on the activity of the Speckled Wood butterfly *Pararge aegeria*. *Oikos*, **42**, 371-377

Shreeve, T.G. & Dennis, R.L.H. (2011) Landscape scale conservation: resources, behaviour, the matrix and opportunity. *Journal of Insect Conservation*, **15**, 179-188

Stamps, J.A., Krishnan, V.V. & Reid, M.L. (2005) Search costs and habitat selection by dispersers. *Ecology*, **86**, 510-518\

Steffan-Dewenter, I. & Tscharntke, T. (2000) Butterfly community structure in fragmented habitats. *Ecology Letters*, **3**, 449-456

Stohlgren, T.J. & Bachand, R.R. (1997) Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology*, **78**, 632-641

Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour*, **56**, 801-809

Tainton, N.M. & Mentis, M.T. (1984) Fire in grassland. *Ecological effects of fire in South African Ecosystems* (ed. by P. de V Booysen and N.M. Tainton), pp 115-147. Springer-Verlag, Berlin.

Terblanche, R.F., Morgenthal, T.L. & Cilliers, S.S. (2003) The vegetation of three localities of the threatened butterfly species *Chrysoritis aureus* (Lepidoptera: Lycaenidae). *Koedoe*, **46**, 73-90

ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO reference manual and user's guide to Canoco for windows: software for Canonical community ordination (version 4.5).* Microcomputer Power, Ithaca

Thomas, J.A. (1984) The behaviour and habitat requirements of *Maculinea nausithous* (the Dusky Blue Butterfly) and *M. teleius* (the Scarce Large Blue) in France. *Biological Conservation*, **28**, 325-347

Tiple, A.D., Padwad, S.V., Dapporto, L. & Dennis, R.L.H. (2010) Male mate location

behaviour and encounter sites in a community of tropical butterflies: taxonomic and site associations and distinctions. *Journal of Biosciences*, **35**, 629-646

Turlure, C., Baguette, M., Stevens, V.M. & Maes, D. (2011) Species- and sex-specific adjustments of movement behavior to landscape heterogeneity in butterflies. *Behavioral Ecology*, **22**, 967-975

Vaidya, V.G. (1969) Investigations on the role of visual stimuli in the egg-laying and resting behaviour of *Papilio demoleus* L. (Papilionidae, Lepidoptera). *Animal Behaviour*, **17**, 350-355

Wood, P.A. & Samways, M.J. (1991) Landscape element pattern and continuity of butterfly flight paths in an ecologically landscaped botanic garden, Natal, South Africa. *Biological Conservation*, **58**, 149-166

Woodhall, S. (2005) *Field guide to butterflies of South Africa*. Struik Nature, Cape Town, South Africa

Chapter 6

General Conclusion

The Mesofilter Concept and Biodiversity Conservation in an Afro-montane Grassland Landscape

Increased emphasis is being placed on understanding the determinants of observed spatial heterogeneity in species richness and composition, as this will greatly optimize conservation planning for both biodiversity maintenance and movement of species under changing climate (Gaston 2000). Indeed, maintaining biodiversity is essential for promoting sustainability of ecosystems into the future (Tilman *et al*. 2006). Following on from this outlook, the mesofilter is a concept that can help explain spatial heterogeneity of species in the landscape (Hunter 2005). Moreover, it is a valuable addition as an operational scale in the contemporary biodiversity and conservation planning toolbox (Schulte *et al*. 2006; Samways & Böhm 2012).

Mountainous areas in South Africa are often areas of high endemism, but also highly threatened, which is why conservation research within these areas is a priority (Clark *et al*. 2011). Here, I set out to explore possible mesofilters for a highly threatened Afro-montane grassland landscape in KwaZulu-Natal, South Africa, as part of the conservation planning (design and management) associated with such landscapes. Specifically, I explored the influence of percentage rock exposure across the landscape as a potential indicator of species richness and species assemblage variability, using a multi-taxon and multi-trophic approach. As this is a montane landscape, I also used elevation as a proxy for microclimatic events (Hodkinson 2005). The study had two basic parts: 1) **if** rockiness contributes to species community structure (the existence of a mesofilter), then 2) exactly **why** rockiness is potentially such a good indicator of species richness and communities, by exploring the functional or behavioural response of the selected taxa to rockiness in the landscape.

Rockiness and species community structure

In *Chapter 2*, I showed the influence of a physical ecosystem element, rockiness, on the species richness and assemblage structure of three key grassland taxa: flora, butterflies and grasshoppers. This finding, where an abiotic surrogate is representative of three key taxa in an

ecosystem, is interesting, as cross-taxon surrogacy has been shown to be generally stronger than surrogates based on environmental data (Rodrigues & Brooks 2007). From a philosophical point of view, I therefore support the idea that environmental surrogates are indeed useful for biodiversity conservation planning, as they can successfully predict areas of conservation concern (Sarkar *et al.* 2005), at least across this studied ecosystem. Furthermore, the concept of the mesofilter as a practical biodiversity conservation tool is validated here, as 1) the rockiness mesofilter adds considerably to our current understanding of species distribution pertaining to certain landscape elements at a small spatial scale, and 2) the rockiness mesofilter is readily quantifiable and easy to map, which would ease land-use decision making in similar areas where species inventories are currently lacking, and development is taking place rapidly. The mesofilter, as studied here, is therefore complementary to fine-filter approaches as it encompasses easily quantifiable variables which are associated with a variety of species. It also complements coarse-filter approaches, as it enables us to establish which broad areas are of protection priority in and among areas set out for potential development. Consequently, I argue that the mesofilter operational scale can be used effectively alongside currently implemented conservation planning operational scales such as fine- and coarse-filter approaches (Hunter 2005; Schulte *et al.* 2006).

Responses of studied taxa to the rocky mesofilter in the landscape

From *Chapter 2*, a key question still remains: why would flora, butterflies and grasshoppers respond to rockiness in the landscape? As briefly outlined in *Chapter 1*, rocks are sedentary and durable ecosystem elements, and we can reasonably assume that species could be adapted to such elements and conditions associated with them. However, there is little information on *why* this should be so.

For flora (*Chapter 3*), this response to rockiness was explained as follows:
- Species within certain *plant growth forms* such as geophytes and perennial grasses had higher association with rockiness and were therefore the main contributors to the observed differences in spatial dispersion of species richness.
- Rockiness creates higher habitat heterogeneity which leads to localised species specialisation through possible confounding factors such as fire and predation (ecological processes).

Details from *Chapter 3* suggest that when there is an abiotic feature such as rockiness in the landscape, it leads to spatial heterogeneity of certain plant functional types, and, from a practical conservation perspective, aids in highlighting plant biodiversity hotspots within these montane grasslands.

For grasshoppers (*Chapter 4*), the response to rockiness was explained as follows:

- Grasshoppers are not necessarily responding to higher rock exposure *per se*, but more towards the environmental conditions created by rockiness within the ecosystem.
- In essence, grasshoppers responded to the plant community structure (vegetation density) and the higher species richness of certain growth forms, especially geophytes and perennial grasses, which are in turn associated with higher rockiness.

The grasshopper dispersion patterns observed in this Afro-montane grassland landscape is thus a function of specialist species which are strongly associated with specific microsite conditions, which in this case, are related to the correlates of the rocky mesofilter.

For butterflies (*Chapter 5*), the response to rockiness was explained as follows:

- Certain behavioural traits are more typical in areas of higher rock exposure, which suggests that rocks are definite visual cues to certain butterflies.
- The physical exploitation of rocks by certain butterflies was distinctive, which emphasise that this response to rocks is highly species-specific.
- Specifically, behaviour associated with thermoregulation, mate-locating, and/or territorial behaviour were the main influences on species being more active in rockier areas.

Consequently, for Afro-montane grasslands the structural component of this habitat is of great importance to butterflies in fulfilling some of their critical life-history strategies, and therefore helps explain their dispersion patterns.

Thesis Synthesis and Application

Collectively, optimized decision-making tools are required that relate to protected area, conservancy, or land-sparing design and management (Sarkar *et al*. 2006). Here I propose that the rocky mesofilter is an important complementary approach to conservation decision-

making in montane grassland ecosystems. However, one of the most critical messages in this thesis, is that although it is important to conserve these rocky areas, as they form an inherent part of the ecology of many taxa, we must also include the lesser rocky areas. This is especially true for butterflies, where the conservation of the entire rocky gradient would conserve most species. In addition, it was clear that elevation in this montane landscape is also an important mesofilter for flora and grasshoppers. Overall these findings suggest that the concept of habitat heterogeneity in biodiversity conservation planning is important. Agricultural intensification is seen as a major driver of spatial heterogeneity loss in ecosystems, with reduced biodiversity for many taxa, requiring the promotion of initiatives which strive to restore habitat heterogeneity of natural areas in agricultural landscapes so as to promote biodiversity conservation (Benton *et al*. 2003). My study was on remnant patches of critically endangered grassland in an afforested matrix, the threatened status of which is in part due to timber production. However, as briefly outlined in *Chapter 1*, there is good reason to reduce the impact of timber production in most areas through the design and management of ecological networks (Samways *et al*. 2010a). My findings for this grassland ecosystem, where good patch quality for many key taxa is strongly associated with rockiness and elevation, supports the argument of Benton *et al*. (2003) to promote habitat heterogeneity in the agricultural landscape, which in this instance would involve optimised design of ecological networks through information obtained from the mesofilter concept (see also Samways *et al*. 2010b). Figure 6.1 is a depiction of a possible design strategy of an ecological network in this Afro-montane landscape according to mesofilters studied here.

Essentially, rockiness is an important departure point from where we can delineate a design or management recommendation for Afro-montane grasslands. In this light, we strive towards a more complete biodiversity conservation toolbox for an ecosystem (*sensu* Schulte *et al*. 2006). As mentioned in *Chapter 2*, any ecosystem can be thought of as having many attributes or features that would be of conservation interest, and mesofilters are only a way of expressing a particular attribute to be used in wildlife conservation evaluation (Usher 1986). I accept that many other mesofilters might also exist in this landscape, the riparian areas being another important one in this instance (Hunter 2005; see Fig. 6.1). Also, many other taxa which also occur in these montane areas, which were not studied here, may not even be associated with rockiness at all. However, for at least the three studied taxa here, we can safely add another tool in the conservation toolbox of this Afro-montane grassland ecosystem.

In addition, this rockiness mesofilter also indirectly indicates the potential for restoration of such montane grassland landscapes in an agricultural system, as is the case with engineering complex habitat structures in restoration initiatives (Ewing 2002; Hough-Snee *et al*. 2011). Lastly, as rockiness in a landscape is an integral structural component of many ecosystems worldwide, this measurable interaction between rockiness and certain taxa, especially since the studied taxa here showed a functional response to rockiness, is likely to have similar value as a mesofilter in such other ecosystems.
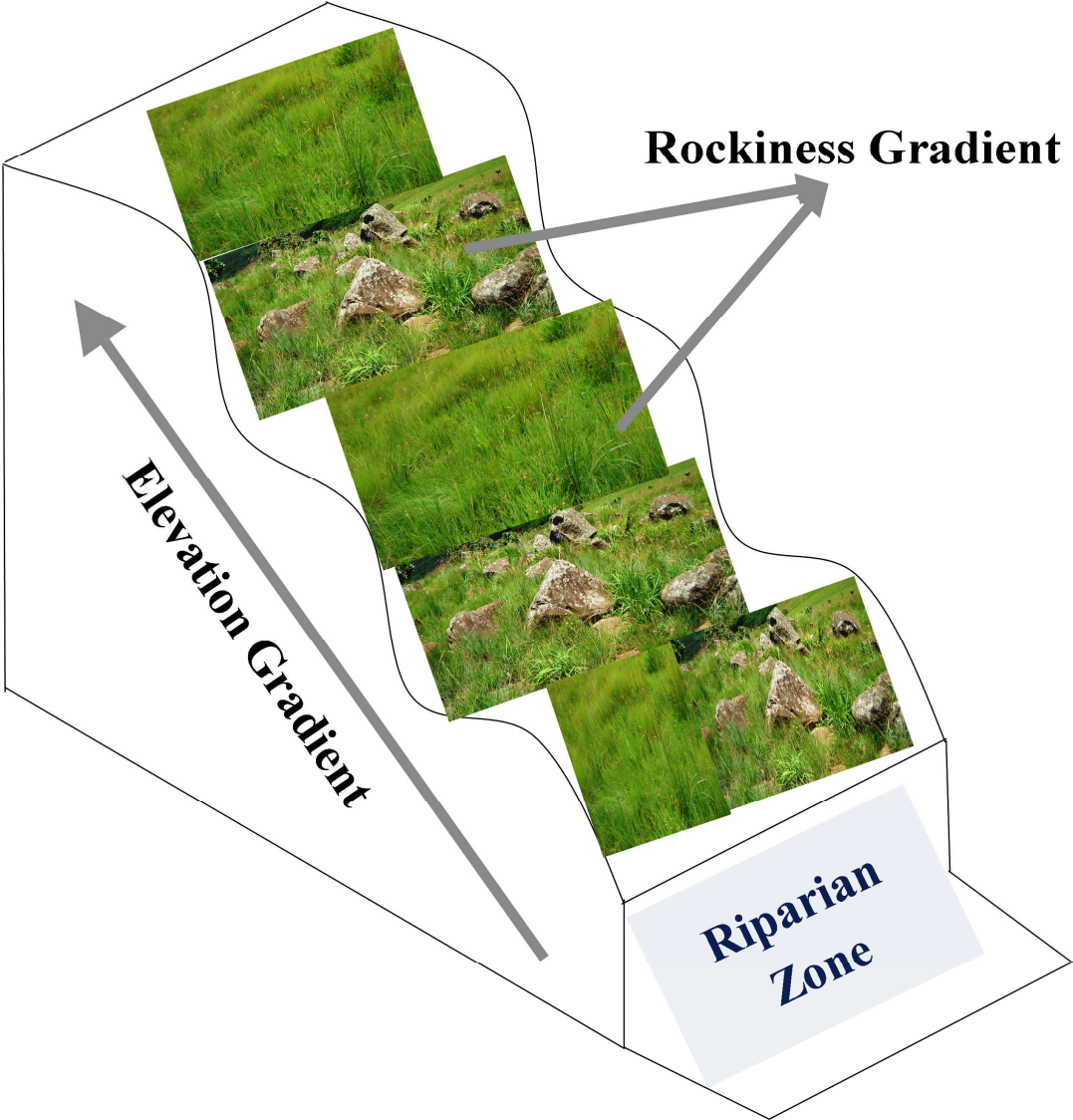
Figure 6.1 A simplified ecological network design for the studied Afro-montane grasslands, within a forestry matrix, according to the rockiness and elevation mesofilters, and another mesofilter, such as the riparian zone

References

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182-188

Clark, V.R., Barker, N.P. & Mucina, L. (2011) The great escarpment of southern Africa: a new frontier for biodiversity exploration. *Biodiversity and Conservation*, **20**, 2543-2561

Ewing, K. (2002) Mounding as a technique for restoration of prairie on a capped landfill in the Puget Sounds lowlands. *Restoration Ecology*, **10**, 289-296

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227

Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews*, **80**, 489-513

Hough-Snee, N, Long, A.L., Jeroue, L. & Ewing, K. (2011) Mounding alters environmental filters that drive plant community development in a novel grassland. *Ecological Engineering*, **37**, 1932-1936

Hunter, Jr., M.L. (2005) A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology*, **19**, 1025-1029

Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 713-737.

Samways, M.J., Bazelet, C.S. & Pryke, J.S. (2010a) Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation*, **19**, 2949-2962

Samways, M.J., McGeoch, M.A. & New, T.R. (2010b) *Insect Conservation: a handbook of approaches and methods*. Oxford University Press, Oxford, UK

Samways, M.J. & Böhm, M. (2012) Hidden in plain view: effective invertebrate conservation for our future world. In: Collen, B., Kemp, R. & Baillie, J.E.M. (eds), *Spineless: status and trends of the world's invertebrates*, Zoological Society of London, UK

Sarkar, S., Justus, J., Fuller, T., Kelley, C., Garson, J. & Mayfield, M. (2005) Effectiveness of environmental surrogates for the selection of conservation area networks. *Conservation Biology*, **19**, 815-825

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A.,

Wilson, K.A., Williams, K.J., Williams, P.H. & Andelman, S. (2006) Biodiversity conservation planning tools: present status and challenges for the future. *Annual Reviews on Environment and Resources*, **31**, 123-159

Schulte, L.A., Mitchell, R.J., Hunter, Jr., M.L., Franklin, J.F., McIntyre, R.K. & Palik, B.J. (2006) Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S. *Forest Ecology and Management*, **232**, 1-11

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632

Usher, M.B. (1986) Wildlife conservation evaluation: attributes, criteria and values. *Wildlife Conservation Evaluation* (ed. M.B. Usher), pp. 3-44. Chapman and Hall, London

Appendix A

Global positioning co-ordinates and topography of sampled sites at Weza, KwaZulu-Natal, South Africa

Site	Latitude	Longitude	Elevation	Aspect
1	30°34.453 S	029°38.887 E	1431 m a.s.l.	South
2	30°34.537 S	029°39.067 E	1420 m a.s.l.	South
3	30°34.488 S	029°39.182 E	1423 m a.s.l.	North
4	30°34.569 S	029°39.867 E	1351 m a.s.l.	South
5	30°34.521 S	029°39.101 E	1422 m a.s.l.	Ridge
6	30°33.942 S	029°41.293 E	1134 m a.s.l.	North
7	30°34.316 S	029°41.596 E	1123 m a.s.l.	Ridge
8	30°32.917 S	029°44.869 E	1049 m a.s.l.	South
9	30°35.314 S	029°40.030 E	1290 m a.s.l.	Ridge
10	30°35.343 S	029°40.301 E	1173 m a.s.l.	North
11	30°35.433 S	029°40.467 E	1135 m a.s.l.	South
12	30°34.945 S	029°40.579 E	1257 m a.s.l.	Ridge
13	30°35.089 S	029°41.342 E	1214 m a.s.l.	South
14	30°34.855 S	029°44.746 E	1102 m a.s.l.	Ridge
15	30°35.996 S	029°39.895 E	1300 m a.s.l.	North
16	30°35.511 S	029°41.547 E	1072 m a.s.l.	North
17	30°37.039 S	029°38.037 E	1610 m a.s.l.	North
18	30°37.313 S	029°37.313 E	1595 m a.s.l.	Ridge

Appendix B

Species accumulation curves for sampled taxa

Flora

Grasshoppers

Butterflies
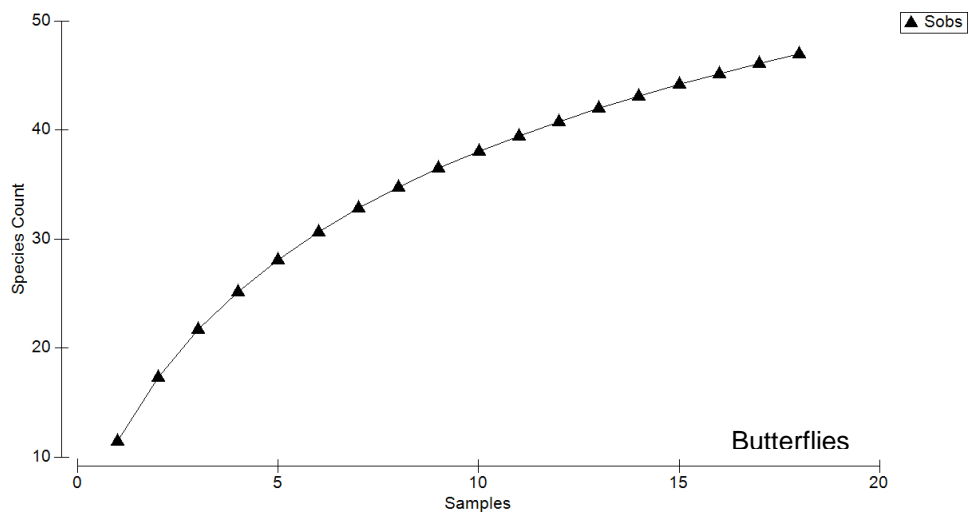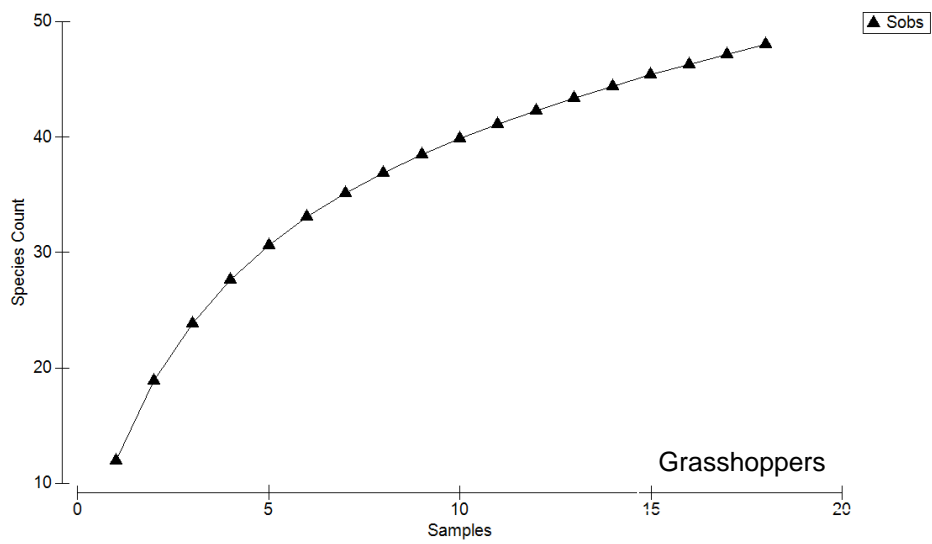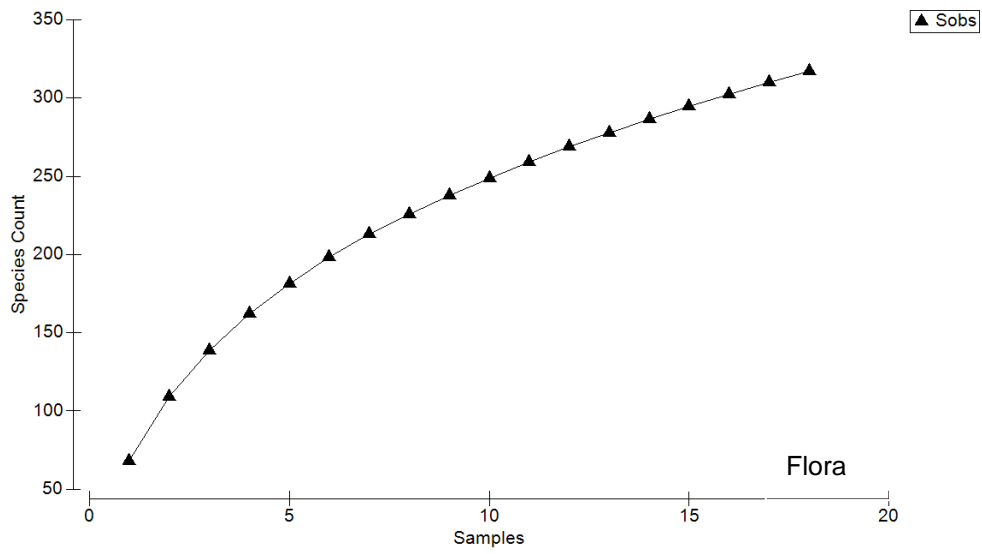
Appendix C

Species list of recorded flora in this study, compiled by family and scientific names

Family	Scientific Name
ACANTHACEAE	*Crabbea sp. 1*
	Barleria monticola
	Thunbergia atriplicifolia
ADIANTACEAE	*Cheilanthes eckloniana*
	Cheilanthes quadripinnata
	Pellaea calomelanos
AGAPANTHACEAE	*Agapanthus campulatus*
AMARYLLIDACEAE	*Brunsvigia grandiflora*
ANACARDIACEAE	*Rhus sp. 1*
	Rhus dentata
	Rhus montana
	Rhus pondoensis
APIACEAE	*Alepidea natalensis*
	Alepidea peduncularis
	Apiaceae sp. 1
	Apiaceae sp. 2
	Centella glabrata
	Centella sp. 1
	Apiaceae sp. 3
APOCYNACEAE	*Asclepiacea sp. 1*
	Asclepias sp. 1
	Asclepias sp. 2
	Asclepias vicaria
	Brachystelma sp. 1
	Pachycarpus appendiculatus
	Pachycarpus sp. 1
	Schizoglossum bidens
ASPARAGACEAE	*Asparagus sp. 1*
ASPHODELACEAE	*Aloe kraussii*
	Aloe maculata
	Bulbine abyssinica
	Kniphofia parviflora
	Kniphofia sp. 1
ASTERACEAE	*Aster bakerianus*
	Athrixia phylicoides
	Athrixia sp. 1
	Berkheya erysithales
	Berkheya rhapontica

Berkheya setifera
Berkheya speciosa
Brachylaena elliptica
Cotula hispida
Denekia capensis
Euryops sp. 1
Gebera sp. 1
Gerbera ambigua
Gerbera piloselloides
Helichrysum acutatum
Helichrysum acutatum
Helichrysum acutatum
Helichrysum alliodes
Helichrysum appendiculatum
Helichrysum auriceps
Helichrysum coriaceum
Helichrysum dasymallum
Helichrysum ecklonis
Helichrysum herbaceum
Helichrysum krebsianum
Helichrysum nudifolium
Helichrysum pilosellum
Helichrysum ruderale
Helichrysum rugulosum
Helichrysum sp. 1
Helichrysum sutherlandii
Helichrysum tenax var. Tenax
Hypochaeris radicata
Osteospermum herbaceum
Osteospermum sp. 1
Othonna natalensis
Senecio sp. 1
Senecio bupleuroides
Senecio coronatus
Senecio decurrens
Senecio erubescens
Senecio glanduloso-pilosus
Senecio inornatus
Senecio othonniflorus
Senecio oxyriifolius
Senecio scitus
Senecio sp. 2
Senecio venosus
Tolpis capensis

	Vernonia capensis
	Vernonia galpinii
	Vernonia hirsuta
	Vernonia natalensis
	Vernonia sutherlandii
	Vernonia thodei
CAMPANULACEAE	*Craterocapsa tarsodes*
	Wahlenbergia huttonii
	Wahlenbergia sp. 1
	Wahlenbergia sp. 1
CARYOPHYLLACEAE	*Dianthus sp. 1*
	Silene burchellii
COMMELINACEAE	*Commelina africana*
CONVOLVULACEAE	*Ipomoea crassipes*
CRASSULACEAE	*Crassula natalensis*
	Crassula setulosa
	Crassula vaginata
CYPERACEAE	*Carex zuluensis*
	Cyperus dives
	Cyperus obtusiflorus
	Cyperus semitrifidus
	Cyperus sp. 1
	Cyperus sphaerocephalus
	Ficinia cinnamomea
	Scirpus ficinioides
DENNSTAEDTIACEAE	*Pteridium aquilinum*
DIPSACACEAE	*Scabiosa columbaria*
DROSERACEAE	*Drosera natalensis*
ERIOSPERMACEAE	*Eriospermum mackenii*
	Eriospermum ornithogaloides
EUPHORBIACEAE	*Acalypha peduncularis*
	Acalypha punctata
	Clutia cordata
	Euphorbia franksiae
	Phyllanthus parvulus
FABACEAE	*Argyrolobium sericosemium*
	Argyrolobium stipulaceum
	Argyrolobium tuberosum
	Aspalathus chortophila
	Aspalathus spinosa
	Chamaecrista mimosoides
	Crotalaria dura
	Crotalaria dura
	Crotalaria globifera

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	Eriosema kraussianum
	Eriosema squarrosum
	Hoffmannseggia sandersonii
	Indigofera hedyantha
	Indigofera hilaris
	Indigofera sp. 1
	Indigofera suffruticosa
	Indigofera tristis
	Lotononis corymbosa
	Lotononis pulchra
	Lotononis sp. 1
	Psoralea abbottii
	Rhynchosia sordida
	Rhynchosia sp. 1
	Rhynchosia sp. 2
	Rhynchosia villosa
	Tephrosia macropoda
	Tephrosia sp. 1
	Tephrosia sp. 2
	Vigna unguiculata
	Zornia capensis
GENTIANACEAE	*Chironia krebsii*
	Sebaea natalensis
GERANIACEAE	*Monsonia grandifolia*
	Pelargonium bowkeri
GESNERIACEAE	*Streptocarpus sp. 1*
HYACINTHACEAE	*Albuca fastigiata*
	Eucomis autumnalis
	Galtonia sp. 1
	Ledebouria ovatifolia
	Ornithogalum graminifolium
	Scilla dracomontana
	Scilla krausii
	Scilla natalensis
	Scilla nervosa
HYPOXIDACEAE	*Hypoxis sp.1*
	Hypoxis acuminata
	Hypoxis argentea
	Hypoxis costata
	Hypoxis hemerocallidea
	Hypoxis rigidula
	Hypoxis sp. 2
	Rhodohypoxis baurii
IRIDACEAE	*Aristea abyssinica*

	Dierama igneum
	Dierama latifolium
	Dierama luteoalbidum
	Gladiolus dalenii
	Gladiolus longicollis
	Hesperantha baurii
	Hesperantha lactea
	Moraea brevistyla
	Moraea inclinata
	Moraea sp. 1
	Moraea spathulata
	Watsonia gladioloides
	Watsonia lepida
	Watsonia densiflora
LAMIACEAE	*Leonotis intermedia*
	Plectranthus colycina
	Stachys natalensis
	Stachys nigricans
LINACEAE	*Linum thunbergii*
LOBELIACEAE	*Lobelia flaccida*
	Lobelia flaccida subsp. Mossiana
MALVACEAE	*Hibiscus aethiopicus*
OPHIOGLOSSACEAE	*Mohria vestita*
ORCHIDACEAE	*Corycium nigrescens*
	Disa stachyoides
	Disperis renibractea
	Eulophia clavicornis
	Eulophia foliosa
	Eulophia ovalis
	Eulophia sp. 1
	Eulophia tenella
	Eulophia zeyheriana
	Habenaria ciliosa
	Habenaria clavata
	Satyrium cristatum
	Satyrium hallackii
	Satyrium longicauda
	Satyrium sphaerocarpum
OXALIDACEAE	*Oxalis depressa*
	Oxalis obliquifolia
	Oxalis smithiana
	Oxalis semiloba
POACEAE	*Alloteropsis semialata*
	Andropogon schirensis

	Aristida congesta subsp. barbicollis
	Aristida transvaalensis
	Bothriochloa insculpta
	Brachiaria deflexa
	Brachiaria serrata
	Cenchrus ciliaris
	Cymbopogon excavatus
	Cymbopogon validus
	Digitaria eriantha
	Echinochloa pyramidalis
	Ellonurus muticus
	Eragrostis capensis
	Eragrostis curvula
	Eragrostis lamaniana
	Eragrostis racemosa
	Harpochloa falx
	Helictotrichon natalense
	Heteropogon contortus
	Hyparrhenia hirta
	Hyparrhenia cymbaria
	Loudetia simplex
	Melinis nerviglumis
	Melinis repens
	Microchloa caffra
	Panicum ecklonii
	Panicum natalense
	Panicum schinzii
	Paspalum dilatatum
	Paspalum notatum
	Pentaschistis natalensis
	Rendlia altera
	Setaria nigrirostris
	Sorghum bicolor
	Sporobolus fimbriatus
	Themeda triandra
	Trachypogon spicatus
	Tricholaena monachne
POLYGALACEAE	*Muraltia lancifolia*
	Polygala confusa
	Polygala hottentotta
	Polygala rehmannii
PROTEACEAE	*Protea dracomontana*
	Protea welwitschii
ROSACEAE	*Rubus ludwigii*

RUBIACEAE	*Anthospermum herbaceum*
	Pentanisia prunelloides
SANTALACEAE	*Thesium pallidum*
SCROPHULARIACEAE	*Buchnera simplex*
	Buchnera sp. 1
	Cycnium racemosum
	Jamesbrittenia breviflora
	Sopubia cana
	Striga bilabiata
THYMELAEACEAE	*Gnidia baurii*
	Gnidia kraussiana
	Gnidia sp. 1
VERBENACEAE	*Verbena sp. 1*

Geophyte presence-absence species list across three rockiness categories. Shaded blocks indicate presence of a species within a category. Indicated in bold are the geophyte species which did not occur in the <8% rockiness category. Nomenclature follows Pooley (2003[1], 2005[2]).

Species	\<8	\<8	\<8	\<8	8-16	8-16	8-16	8-16	8-16	\>16	\>16	\>16	\>16
Agapanthus campulatus			■				■		■				
Albuca fastigiata				■		■		■	■	■	■	■	■
Brunsvigia grandiflora					■								
Bulbine abyssinica							■				■		
Cheilanthes eckloniana													■
Cheilanthes quadripinnata									■				
Corycium nigrescens						■	■			■			
Dierama igneum		■				■	■				■		
Dierama latifolium						■			■				
Dierama luteoalbidum		■											
Eriospermum mackenii	■								■				
Eriospermum ornithogaloides													■
Eucomis autumnalis			■	■			■		■				
Eulophia clavicornis					■				■			■	
Eulophia foliosa									■				
Eulophia ovalis				■			■						
Eulophia tenella							■						
Eulophia zeyheriana										■	■	■	■
Gladiolus dalenii	■		■	■		■	■	■	■	■	■	■	■
Gladiolus longicollis													
Habenaria ciliosa					■								
Habenaria clavata											■		
Hesperantha baurii													■
Hesperantha lactea													
Hypoxis acuminata			■			■							
Hypoxis argentea	■	■					■	■	■	■	■	■	■
Hypoxis costata			■				■	■			■		
Hypoxis hemerocallidea	■										■		
Hypoxis rigidula			■	■					■		■	■	■
Ledebouria ovatifolia							■	■			■		
Mohria vestita				■						■			

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[1] Pooley, E. (2003) Mountain flowers: a field guide to the flora of the Drakensberg and Lesotho. The Flora Publications Trust, Durban, South Africa

[2] Pooley, E. (2005) A field guide to wildflowers: Kwazulu-Natal and the eastern region. The Flora Publications Trust, Durban, South Africa

Ornithogalum graminifolium

Oxalis depressa

Oxalis obliquifolia

Oxalis semiloba

Oxalis smithiana

Pelargonium bowkeri

Pelargonium luridum

Pellaea calomelanos

Rhodohypoxis baurii

Satyrium cristatum

Satyrium hallackii

Satyrium longicauda

Satyrium sphaerocarpum

Scilla dracomontana

Scilla krausii

Scilla natalensis

Scilla nervosa

Watsonia densiflora

Watsonia gladioloides

Perennial grass presence-absence species list across three rockiness categories. Shaded blocks indicate presence of a species within a category. Nomenclature follows van Oudtshoorn (2009)[3].

Species	<8	<8	<8	<8	8-16	8-16	8-16	8-16	8-16	>16	>16	>16	>16
Alloteropsis semialata		■	■		■				■			■	■
Andropogon schirensis	■										■		
Bothriochloa insculpta	■										■		
Brachiaria serrata							■						
Cenchrus ciliaris	■	■	■	■	■	■		■	■	■	■	■	■
Cymbopogon excavatus			■		■	■	■		■	■		■	
Cymbopogon validus	■		■							■	■		
Cyperus dives													
Cyperus obtusiflorus	■		■						■	■	■	■	■
Cyperus semitrifidus	■												
Cyperus sphaerocephalus							■						
Digitaria eriantha		■						■					
Echinochloa pyramidalis	■				■	■					■		
Elionurus muticus							■						
Eragrostis capensis									■			■	
Eragrostis curvula		■	■	■	■	■	■			■		■	
Eragrostis lehmanniana													
Eragrostis racemosa		■			■	■	■		■	■	■		■
Ficinia cinnamomea	■				■	■	■	■		■	■	■	■
Harpochloa falx					■	■	■	■		■		■	
Helictotrichon natalense	■	■			■	■				■			
Heteropogon contortus	■		■	■	■	■		■	■	■			
Hyparrhenia cymbaria		■				■							
Hyparrhenia hirta										■	■	■	
Loudetia simplex	■	■		■	■	■			■		■	■	
Melinis nerviglumis										■	■		■
Microchloa caffra		■			■		■		■		■	■	
Panicum ecklonii	■				■					■		■	
Panicum natalense	■	■			■						■		
Paspalum dilatatum							■						
Paspalum notatum									■				
Rendlia altera		■	■	■	■		■			■	■	■	■
Scirpus ficinioides	■								■			■	
Setaria nigrirostris							■						
Sporobolus fimbriatus									■				
Themeda triandra	■	■	■	■	■	■	■	■	■	■	■	■	■
Tricholaena monachne										■			

[3] Van Oudtshoorn, F. (2009) Guide to grasses of southern Africa. Briza Publications, Pretoria, South Africa

Appendix F

Butterfly species list and abbreviations used for CANOCO analysis

Species Name	Abbreviation
Acrea horta	Acho
Acrea neobule neobule	Acnn
Acrea violarum	Acvi
Actizera lucida	Aclu
Aeropetes tulbaghia	Aetu
Alaena amazoula amazoula	Alaa
Aloeides aranda	Alar
Aloeides oreas	Alor
Belenois aurota aurota	Beaa
Belenois creona severina	Becs
Belenois zochalia zochalia	Bezz
Byblia ilithyia	Byil
Cassionympha cassius	Caca
Catacroptera cloanthe cloanthe	Cacc
Catopsilia florella	Cafl
Cupidopsis cissus cissus	Cucc
Cupidopsis jobates jobates	Cujj
Danaus chrysippus aegyptius	Daca
Dixeia charina charina	Dicc
Eretis umbra umbra	Eruu
Eurema brigitta brigitta	Eubb
Eurema hecabe solifera	Euhs
Eurytela hiarbas angustata	Euha
Gegenes niso niso	Genn
Hyalites esebria esebria	Hyee
Junonia hierta cebrene	Juhc
Junonia orithya madagascariensis	Juom
Kedestes chaca	Kech
Lampides boeticus	Labo
Leptomyrina gorgias gorgias	Legg
Leptotes pirithous pirithous	Lepp
Metisella metis	Meme
Papilio demodocus demodocus	Padd
Papilio nireus lyaeus	Panl
Paralethe dendrophilus	Pade
Pardopsis punctatissima	Papu
Precis archesia archesia	Praa

Precis octavia sesamus f. *natalensis*[4]	Pron
Precis octavia sesamus f. *sesamus*	Pros
Pseudonympha poetula	Pspo
Sevenia natalensis	Sena
Spialia diomus ferax	Spdf
Stygionympha curlei	Stcu
Thestor basutus	Thba
Tsitana tsita	Tsts
Unknown spp	Unkn
Vanessa cardui	Vaca

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[4] I kept the two *Precis* forms separate, as they show considerable morphological differences in both colour and pattern, and according to my observations in the field, are also reproductively separate. However, this made no difference to the key findings of this study.